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Title	AN EXTRAORDINARY PUPILLARIAL GENUS OF SCALE INSECTS ASSOCIATED WITH ANNONACEAE IN TROPICALASIA (STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)
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**AN EXTRAORDINARY PUPILLARIAL GENUS OF  
SCALE INSECTS ASSOCIATED WITH ANNONACEAE  
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By SADAO TAKAGI

*Abstract*

TAKAGI, S., 2008. An extraordinary pupillarial genus of scale insects associated with Annonaceae in tropical Asia (Sternorrhyncha: Coccoidea: Diaspididae). *Ins. matsum. n. s.* 64: 81–115, 19 figs.

*Annonogena*, gen. nov., is erected on the basis of four species, *A. acutilobata*, sp. nov. (type species), from Mindoro Island and *A. rotundilobata*, sp. nov., *A. echinata*, sp. nov., and *A. aristata*, sp. nov., from Borneo Island, all occurring on plants of the family Annonaceae. The genus is pupillarial, with the adult female extremely simplified in external structures; the second-instar female is peculiarly featured, and the second-instar male lacks well-formed marginal appendages. The taxonomic position of the genus, therefore, is not easily determinable. The genus is referred to the tribe Parlatoriini mainly by means of excluding other possibilities. It is compared with *Parlatoria proteus*, the type species of *Parlatoria*, and the two known species of the pupillarial parlatoriine genus *Ligaspis*, and probable evolutionary changes from an ordinary parlatoriine form to the genus are discussed.

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*Contents.* Introduction — *Annonogena*, gen. nov. — *Annonogena acutilobata*, sp. nov. — *Annonogena rotundilobata*, sp. nov. — *Annonogena echinata*, sp. nov. — *Annonogena aristata*, sp. nov. — Taxonomic position — Evolutionary changes — References — Corrections — Figures.

Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia, Scientific Report.

## INTRODUCTION

In the current classification, the superfamily Coccoidea, comprising coccids, mealybugs, scale insects, and others, is referred to the Sternorrhyncha under the hemimetabolous order Homoptera or Hemiptera (s. lat.). The males, however, have the stages of prepupa and pupa between the last nymphal stage and the adult stage. Thus, the male Coccoidea, together with the Thysanoptera and Aleyrodoidea, 'constitute the aberrant Hemimetabola and, in fact, are holometabolous exopterygotes. The somewhat similar life histories of members of these taxa have evolved independently through selection for sessile or cryptic juvenile feeding. This has resulted in a level of structural divergence between young and adults requiring the presence of two or three transitional pupal instars to bridge the structural gap between the two' (Heming, 2003). The adult males of the Coccoidea do not feed, with the mouth-parts degenerated to a trace, and die soon after finishing copulation. They disperse, but their dispersal has only a secondary significance, being effective within the range of dispersal made by the females mainly or exclusively during the crawling period of the first instar. (Exceptionally, adult males transport female crawlers, thus playing a critical role in dispersal.)

The female coccoids have another process of ontogeny: the adults emerge immediately from the last nymphal stage and continue to feed and grow, increasing in body size considerably and changing in body shape slightly or remarkably. In this respect the adult females represent an extended nymphal stage: in fact, they have no trace of wings and usually are similar to the nymphs of the preceding instar in general external morphologies. Quite different from the ephemeral adult males, the persisting adult females occupy a central position in adaptation to the sedentary juice-sucking coccoid life on plants. The current classification of the Coccoidea is largely based on characters of the neotenic adult female. This is primarily because specimens of the adult female are easily accessible owing to the persistence of this stage, but is not insignificant biologically on account of the dominative position of the stage in adaptive evolution. In this regard, the classification of this insect group is eminently gradistic.

The Diaspididae have two nymphal instars: the main role of the first-instar nymphs is dispersal, and they are provided with well-developed antennae and legs, and in many species also with a pair of long caudal setae, which are supposed to contribute to their dispersal by air currents; the second instar is devoted to feeding and growth, with tubercular antennae and no legs. The adult females, also with tubercular antennae and no legs, are generally provided with abundant wax-secreting ducts and well-developed marginal appendages; these features show taxon-specific patterns and must have developed primarily in association with the habit of test formation. In principle, the second-instar nymphs (except the heteromorphic male nymphs) have ducts and appendages similar to those of the adult females, but the ducts are usually much reduced in number in the female nymphs, reflecting the fact that in the female the greater part of the test is formed by the adult. In the male, the test is completed during the second instar, which is provided with abundant wax-secreting ducts; in general, however, the male test is much smaller than the female test.

Exceptions to the above are found in part of the family: the 'pupillarial' or 'cryptogyne' forms of the female do not grow in the adult, which remains under or within the sclerotized, often enlarged, exuvial cast of the second-instar nymph. The external structures of the pupillarial adult females as compared with those of related

non-pupillarial forms are apparently simplified and modified in various ways and in various degrees, and especially reductive in the wax-secreting ducts and marginal appendages. This is natural, because the pupillarial adult females are no longer engaged in test formation. Thus, in the pupillarial forms, the adaptive significance of the adult female should be changed greatly, the role of the stage being largely restricted to reproduction. The pupillarial species are classified into their own genera, which are recognized usually by combining characters of the simplified adult female with those of the conservative second-instar female. As a rule, the relationships of the pupillarial genera to non-pupillarial ones are presumed on the basis of the second instar. In this way the pupillarial genera are referred to various tribes of the family, and this means that the pupillarial mode of life emerged independently among the tribes (and probably also within the tribes at least to some extent). The small tribes Thysanaspidini and Leucaspidini are represented only by pupillarial genera. The nymphal instars reveal that these tribes are primitive taxa in the subfamily Aspidiotinae, and the view may be adopted that they are remnants of larger groups, which should have once diversified to embrace pupillarial and non-pupillarial genera. This view implies that the pupillarial mode of life has its own advantage in survival under some conditions. The small family Halimococcidae, which is closely related to the Diaspididae, is composed exclusively of pupillarial forms, which fact suggests that the extant forms of the family are also survivors of a larger group.

The tribe Parlatoriini is rich in pupillarial genera, which are referred to the tribe mainly on the basis of the parlatoriine pattern of characters maintained in the second instar. The new genus proposed in this paper is assigned to the Parlatoriini. However, in discordance with the general rule, the second-instar female bears no trace of the parlatoriine pattern and, instead, is provided with quite peculiar features. The second-instar male shows another pattern of characters, which is not obviously parlatoriine, either. An attempt will be made to explain why the genus is referable to the Parlatoriini. If the tribal position adopted in this paper is correct, this genus shows that pupillarial forms sometimes greatly change not only in the adult female but also in the second instar female and male.

*Annonogena*, gen. nov.

Type species. *Annonogena acutilobata*, sp. nov.

A pupillarial genus, the adult female being entirely enclosed within the second-instar exuvial cast, which is strongly sclerotized and plump and thus may appear like a minute plant seed. The male constructs a good test. The first-instar exuvial cast of the male is elliptical and of the bivalve type: the dorsal and ventral surfaces are separated from each other along the margin except for an anterior portion, thus remaining attached to each other. The known species occur on the lower surface of the leaves. The females are found usually on the lateral sides of the midrib and other veins. The male tests are detached from the leaf surface except for the anterior end, with the ventral as well as the dorsal portion formed well; they are white, elongate, parallel-sided, and flat dorsally.

*Adult female.* Body elongate elliptical, rounded on both ends, membranous, with segmentation obscure except on ventral surface of prepygidial abdomen; pygidium appearing to comprise fourth or fifth and succeeding abdominal segments, slightly



projecting beyond general body outline, little sclerotic on dorsal surface, finely striate longitudinally on ventral surface in a broad marginal region, minutely serrate marginally in correspondence to the striae. Antennae occurring within head margin, set close together, each with a rather thick seta. No disc pores associated with spiracles. Small ducts occurring submarginally in anterior region of body: in a group anteriorly to the level of the anterior spiracle [termed 'antespiracular ducts' in this paper]; in another group between the levels of the anterior and posterior spiracles ['interspiracular ducts']; a few present or absent posteriorly to the level of the posterior spiracle (probably on base of abdomen) ['postspiracular ducts']. Anus large, situated about centre of pygidium. No perivulvar disc pores. Small, slender, much elongated ducts occurring on pygidial margin (occasionally absent); orifices hardly visible, but in some cases opening apparently on ventral surface. No trace of marginal appendages on pygidium and prepygidial segments. No setae on dorsal surface except for some short setae occurring on pygidial margin.

*Second-instar female.* Body elongate obpyriform; thoracic and abdominal segments indistinct, suggested by setae on ventral surface; dorsal setae mostly lacking. Pygidium appearing to comprise fifth and succeeding abdominal segments, produced beyond general body outline, rounded marginally. Antennae set close together, each with a rather thick seta. No disc pores associated with spiracles. Many small ducts scattered submarginally on prepygidial ventral surface. Dorsal surface of pygidium forming a disc-like structure ['dorsal disc'], which is well demarcated basally and, in the exuvial cast, dehisces except on the base to form an operculum for copulation and the egress of crawlers; dorsal disc or operculum depressed obovate in outline, sclerotized, sulcate transversely on base, and roughly reticulate on a narrow or broad submarginal area, the sulci curving posteriorly to merge into the reticulation. The free margin of the operculum is framed with a continuous row of many sclerites ['marginal sclerites'], which are nearly square or elongate (when elongate, mostly aristate) or produced to form conical or rounded lobular processes ['dorsal lobules']. Anus situated posteriorly to centre of dorsal disc. Marginal area of ventral surface of pygidium curved to meet dorsal disc, thus forming a narrow brim, which is complete throughout the pygidial margin or broadly interrupted medially; produced to form many well-developed conical or rounded lobular processes ['ventral lobules'], which occur in a continuous row in parallel to the row of dorsal lobules and are larger than the dorsal lobules, mostly with the apical part folded on the upper surface; or produced to form a short and broad membranous flap, which is divided into many sections by rows of perforations running through the brim and flap ['perforated flap'].

*Second-instar male.* Body elliptical, with both ends broadly rounded. Pygidium comprising sixth and succeeding segments (as interpreted rather tentatively), rugged marginally, with broad prominences suggesting rudimentary trillae ['lobes' in authors]. Prepygidial region of abdomen distinctly notched segmentally to form lateral lobes, with intersegmental sutures clearly visible on both surfaces. Antennae situated within head margin, separated from each other by a space as wide as frame of mouth-parts, each with a seta. No disc pores associated with spiracles. Anus situated at or somewhat posteriorly to centre of pygidium. Macroducts of the two-barred type present segmentally not only on dorsal surface but also on ventral surface, occurring marginally and submarginally on second to seventh abdominal segments, and submedially on posterior abdominal segments. Slender ducts occurring marginally, opening on dorsal or ventral surface, 1 in each of anterior and posterior lateral corners of second to seventh abdominal segments,

at times also in posterior lateral corner of first segment; a pair at apex of pygidium, probably belonging to eighth segment; most of these ducts, especially on prepygidial abdomen, accompanied each with a small process tending to be rugged apically (so that these ducts may represent rudimentary pectinae ['plates' in authors]). No gland spines, nor gland tubercles. Dorsal submedian setae absent on posterior abdominal segments.

*Remarks.* Four species are recognized as members of the genus, one from Mindoro Island and the other three from Borneo Island. In the second-instar female, two of these species are peculiar in having the dorsal and ventral lobules on the pygidium, and the other two are extraordinary in having the perforated flap; one species is equipped with a number of spinous processes in the prepygidial region, whereas the other three have no trace of such processes. The genus as composed in the present paper, therefore, may appear heterogeneous. The four species are referable to the same genus on the evolutionary interpretations of these peculiar features given in the section Evolutionary changes. In other features of the second-instar female, especially in the sulcate-reticulate dorsal disc, the four species are closely similar. In the adult female and the second-instar male, too, they are very similar. They agree in their association with plants of the family Annonaceae.

One of the species was found in the laboratory under a binocular microscope, when specimens of another scale insect occurring on the same plant material were in preparation. The species of *Annonogena* are minute in body size, and may easily be overlooked in the field unless when occurring in high density. Further species of the genus should exist in tropical Asia, especially in the botanical region Malesia. This genus may be worthy of attention for its possible host expansion from wild Annonaceae onto fruit trees of *Annona*, custard-apple and others, which are native to tropical America and now widely cultivated in the tropics of the world.

The second-instar exuvial cast of the female is strongly sclerotized, so that it is not easy to take out the adult female from the exuvial cast, which is too minute to handle. In the four species, the adult females are very simplified in external structure; the second-instar males are uniform, and two of the four species are not clearly distinguishable from each other in this stage. The four species are recognized mainly on the basis of their second-instar females. Exuvial casts of the second-instar female, therefore, are designated as the holotypes of the four species.

The holotype of the type species is deposited in the collection of the Natural History Museum, University of the Philippines at Los Baños, and the holotypes of the other three species are preserved in the collection of Entomology Division, Forest Research Institute of Malaysia.

In the descriptions of the species, the abbreviations 'abd I–VII' stand for the first to seventh abdominal segments. The terms 'trullae' and 'pectinae' are used in place of 'lobes' and 'plates' in authors; the latter set of terms is widely adopted in describing marginal appendages, but these terms bear general meanings, too, and sometimes are applied to other features.

*Annonogena acutilobata*, sp. nov.

*Material examined.* Collected near Villa Flor, Puerto Galera, Mindoro Island, the Philippines, on *Artabotrys cumingiana* (identified by Dr Edwino S. Fernando, University of the Philippines at Los Baños), 15.VIII.1994 [94PL-46]. About 20 specimens of the adult female were prepared, but

they are more or less shrunk or distorted and the ducts have not always been counted exactly; four teneral specimens and a number of exuvial casts of the second-instar female have been examined; the second-instar male is described on the basis of about 15 specimens.

*Adult female* (Fig. 1). Antespiracular submarginal ducts 3–6 and interspiracular 3–5 on each side; no postspiracular ducts. Anterior spiracles each usually with 1 microduct just posteriorly to peritreme. Pygidium with an irregularly undulate, partly reticulate, linear pattern on dorsal margin; usually with 1 or 2 marginal ducts on each side towards apex.

*Second-instar female* (Figs 2–4). Prepygidial region of body with about 30 ducts strewn submarginally on each side; some ducts in a rather broad space between antennae; a few ducts posteriorly to each spiracle. Dorsal disc of pygidium sulcate except for a narrow submarginal area, which is reticulate; pygidium with dorsal and ventral lobules, which are pointed apically; dorsal lobules 26 or so in total; ventral lobules much larger than dorsal lobules, 16 or so in total. Exuvial cast with dorsal surface of prepygidial region thickly strewn with irregularly shaped small areolae except on a broad marginal area.

*Second-instar male* (Fig. 5). Pygidium apically with a pair of low broad prominences separated from each other by a space and tending to be sclerotic marginally (probably representing median trullae). Dorsal macroducts: 1 occurring near margin and 1 submedially along supposed posterior border of abd VII; 2 near margin and 1 submedially along supposed posterior border of VI; on each of II–V, 1 near margin and 1 submarginally along posterior border, and 1 on lateral margin, of segment. Ventral macroducts arranged in rows arising near margin halfway between anterior and posterior borders of segments: 3 on abd VII; 2 on VI; 3, rarely 2, on V; 3, rarely 2, on IV; 3 on III; 3, at times 2, on II; 1 submarginal ventral macroduct on VI and at times also on V; 1 submedian ventral macroduct usually present on VI. Anterior region of body with macroducts occurring on margin and appearing on dorsal or ventral surface in mounted specimens: 2 on abd I; 3 on metathorax; 3, at times 2, on mesothorax; 1 on prothorax. Abd IV and V each with 1 submedian dorsal microduct; abd II–V each with 1 submedian ventral microduct, also VI with 1 when without submedian ventral macroduct; 2–4 microducts on margin anterior to the level of the anterior spiracle; 1–3 microducts posteriorly to interantennal space; a pair of microducts laterally to apex of rostrum; 1 microduct near peritreme of each spiracle, 1 between posterior spiracle and body margin; abd I without a slender marginal duct in posterolateral corner.

*Annonogena rotundilobata*, sp. nov.

*Material examined.* Collected in Taman Bako [Bako National Park], Sarawak (Borneo Island), Malaysia, on *Friesodielsia* sp. (identified by Mr K. M. Kochummen, Forest Research Institute of Malaysia), 11.X.1991 [91ML-132]. About 10 specimens of the adult female were mounted, but none of them are in good condition; six teneral specimens and some exuvial casts of the second-instar female have been examined; the second-instar male is described on the basis of 15 specimens.

*Adult female* (Fig. 7A). Very similar to adult female of *A. acutilobata*, but distinguishable in having a reticulate linear pattern on a narrow marginal area of pygidial dorsum. Antespiracular submarginal ducts 2–7, interspiracular 2 or 3, and postspiracular 1 or 2 (occasionally absent ?) on each side of body. Anterior spiracles each with 1

microduct just posteriorly to peritreme. Marginal ducts of pygidium present or absent, when present 1 or 2 on each side towards apex.

*Second-instar female* (Fig. 7B). Very similar to the second-instar female of *A. acutilobata*, but is distinguishable mainly in the dorsal and ventral lobules of the pygidium rounded apically. No areolation has been observed on the dorsal surface of the exuvial cast.

*Second-instar male* (Fig. 8). Very similar to the second-instar male of *A. acutilobata*. Dorsal macroducts as in *A. acutilobata* in number and arrangement. Ventral macroducts: abd VI always with 1 submedian macroduct in addition to 1 submarginal macroduct and 2 in a row arising on margin; abd V usually with 1 submarginal macroduct in addition to 3 in a row arising on margin; abd IV with 3 or 4, III with 2 or 3, and II with 2 macroducts in a row arising on margin of each segment. No microduct has been observed laterally to the rostrum; 2–5 microducts on margin anterior to the level of the anterior spiracle.

*Remarks.* This species is closely similar to *A. acutilobata*, but is regarded as distinct on account of the fact that it is distinguishable not only in the second-instar female but also in the adult female.

*Annonogena echinata*, sp. nov.

*Material examined.* Collected in Taman Kinabalu [Kinabalu National Park], Gunong Kinabalu, at an altitude of ca. 1500m, Sabah (Borneo Island), Malaysia, on *Fissistigma kingi* (identified at Forest Research Centre, Sabah), 7.X.1988 [88ML-67, -68]. About 10 specimens of the adult female were mounted, but all of them are not in good condition. The second-instar female is represented only by exuvial casts. The description of the second-instar male is based on about 15 specimens.

*Adult female* (Fig. 9A). Antespiracular submarginal ducts 4–6 and interspiracular 2–4 on each side; no postspiracular ducts have been observed. No microducts associated with spiracles. Pygidium with rudimentary lines forming an obscure pattern on dorsal margin; marginal ducts 5–10 on each side, 11–19 in total.

*Second-instar female* (exuvial cast) (Figs 9B and 10). Prepygidial region equipped with a number of processes over a broad pleural area, which are swollen basally and abruptly narrowed to form an elongate spinous apical part; with about 20 ducts scattered submarginally on ventral surface on each side. Dorsal disc reticulate on a broad marginal area, the margin composed of a continuous series of about 24 sclerites, which are roughly square. Curved brim of ventral surface of pygidium complete, with a perforated flap; divided into about 20 sections by rows of perforations, which extend onto the flap.

*Second-instar male* (Fig. 11). Pygidium apically with a pair of low sclerotic prominences (probably representing median trullae). Dorsal macroducts nearly as in *A. acutilobata*, but no submedian macroduct on abd VI (1 microduct occurring at this site, instead), and no submarginal macroduct on abd II and often also on III. Ventral macroducts: abd VI always with 1 submedian macroduct in addition to 1 or rarely 2 submarginal macroducts and 2 macroducts in a row arising near margin; usually 3 in a row arising near margin on each of III–V, rarely 2 or 4 on V and 4 on IV; usually 2, rarely 1, on II. Microducts absent near anterior spiracles; 2, rarely 4, microducts between posterior spiracle and body margin; 2–4 microducts on margin anterior to the level of the anterior spiracle, 1 of them being isolated in front of the others; 1 or 2 microducts posteriorly to interantennal space; a pair of microducts laterally to rostrum.

*Remarks.* This species is readily distinguishable from the other three in having an echinate body in the second-instar female.

*Annonogena aristata*, sp. nov.

*Material examined.* Collected in Kawasan Pemuliharaan Lembah Danum [Danum Valley Conservation Area], Tawau, Sabah (Borneo Island), Malaysia, on *Ellipeia* sp. (identified at Forest Research Centre, Sabah), 23.X.1988 [88ML-188]. Found incidentally when specimens of *Sclopetaspis danumensis* occurring on the same plant material were in preparation. Five exuvial casts of the second-instar female were mounted, but they are not in good condition; the description of the second-instar male is based on two specimens.

*Adult female.* No entire specimens have been available. The pygidium of an adult female protruding from one of the mounted exuvial casts of the second-instar shows a total of 9 marginal ducts and no trace of an undulate or reticulate linear pattern.

*Second-instar female* (exuvial cast) (Fig. 12). Prepygidial region plain, not areolate, nor echinate; with about 30 ducts scattered submarginally on each side. Dorsal disc tending to be reticulate extensively; margin with a continuous row of about 38 sclerites, which are oblong and apically aristate except for some ones occurring towards the base of the pygidium. Curved brim of ventral surface of pygidium complete, with a perforated flap; divided into about 20 sections by rows of perforations, which extend onto the flap.

*Second-instar male* (Figs 13 and 14). Pygidium apically with a pair of rather prominent, sclerotized, dentate processes, which may be interpreted as median trullae; another less prominent pair may represent the second trullae. Dorsal macroducts as in *A. acutilobata* except for 1 submedian macroduct occurring on abd V (on which, therefore, no submedian microduct occurs). Ventral macroducts nearly as in *A. acutilobata*, but 1 submedian and 1 submarginal macroduct occurring on each of abd V and VI (1 submarginal macroduct on one side of IV in one specimen); 3 near margin on each of II and III. Submedian ventral microducts: 1 on each of abd II–IV (on V and VI replaced by macroducts). A group of 12–16 microducts occurring marginally just anteriorly to the level of the anterior spiracle, 1 isolated microduct anteriorly to the group; 1 microduct posteriorly to peritreme of anterior spiracle; 2 microducts near peritreme of posterior spiracle; 2 microducts posteriorly to interantennal space; no microducts laterally to rostrum; a slender duct in posterolateral corner of abd I (in addition to the slender marginal ducts on the succeeding segments).

*Remarks.* In the second-instar female, this species is commonly characterized with *A. echinata* in having a perforated flap on the curved brim of the ventral surface of the pygidium, but it is easily distinguishable from the latter in having no spinous processes in the prepygidial region and in having aristate marginal sclerites on the dorsal disc of the pygidium. In the second-instar male, this species is readily recognizable in having a group of many microducts on the margin just anteriorly to the level of the anterior spiracle.

TAXONOMIC POSITION

It is hardly possible to decide the taxonomic position of *Annonogena* on the basis of the adult female and the second-instar female in spite of the fact that these stages are generally used for classifying pupillarial diaspidids. In this genus, the adult

females are extremely simplified, and the second-instar females are quite unique in having the dorsal and ventral lobules in two species and the perforated flap in the other two. The second-instar females in all these species are also remarkable in having the sulcate-reticulate dorsal disc or operculum. Exuvial casts bearing a distinct operculum on the pygidium are known in some other pupillarial forms of scale insects: the Halimococcidae, a small family closely related to the Diaspididae, and also several genera of the Diaspididae, e.g., *Anotaspis*, *Radionaspis*, and *Thysanaspis* (in *Anotaspis* and *Thysanaspis*, however, the operculum is ventral). The taxonomic positions of these operculum-bearing diaspidids are not easily clarified. *Thysanaspis* was supposed to represent a very primitive evolutionary level in the subfamily Aspidiotinae on the basis of the nymphal stages, and the tribe Thysanaspidini was erected to accept it (Takagi, 2002). It is not knowable whether *Annonogena* arose from any operculum-bearing pupillarial scale insect or evolved to have an operculum independently. In any case, the genus should have greatly changed from ordinary diaspidids in association with the pupillarial mode of life not only in the adult female but also in the second-instar female.

The first-instar nymphs of both sexes and the succeeding instars of the male are free from the pupillarial mode of life, and their characters may be expected to be conservative, at least relatively, and to afford evidence to show the taxonomic position of *Annonogena*. In the family, only a limited number of species have been examined in detail for their first-instar nymphs, which, so far as known, are not always uniform in the same higher taxon, and it is still premature to illustrate a general pattern of characters and its variation in this stage for each higher taxon.

In many species of the family, the female and male nymphs of the second instar are similar; usually the male nymphs have much more numerous ducts, and the sexual dimorphism may involve other features, too. In the Diaspidini, the Odonaspidini, and the Smilacicolini, male nymphs usually exhibit patterns of characters remarkably different from those of the conspecific female nymphs and adults. Such heteromorphic male nymphs of the second instar may be useful especially in discussing taxonomic positions, because they are interpreted to be primitive or atavistic as compared with the adult females, which are much modified adaptively.

The adult male, the stage of Heming's (2003) 'holometabolous exopterygotes', is drastically different from the nymphs and adult female in body structure, thus affording a suit of characters that are mostly foreign to the nymphs and adult female. So far as known, the adult males of the Diaspididae are fairly uniform as compared with the adaptively diversified adult females, reflecting their restricted role in the life history. Furthermore, occasional apterous adult males are much simplified in body structure. Routine taxonomic descriptions do not include the adult male mainly because of its ephemeral appearance, which makes material of this stage not readily obtainable.

#### *First instar*

Some specimens of the first-instar female and male of *A. acutilobata* have been examined (Fig. 6). They have the tibia and tarsus of each leg fused together and lack submedian dorsal setae on all the abdominal segments in the female and on the fourth and succeeding abdominal segments in the male. In having these characters, *Annonogena* is referable to the group comprising the tribes Aspidiotini, Odonaspidini, and Parlatoriini, all belonging to the subfamily Aspidiotinae, and is excluded from the other tribes of the subfamily and also from the Diaspidinae. The first-instar nymphs of the Aspidiotinae



have five-segmented antennae, which are not uniform throughout the subfamily in the relative lengths of the segments. Especially, in the Aspidiotini the fifth segment tends to be much elongated and in the Odonaspidini the third segment is noticeably long as compared with the second and fourth. *Annonogena* has the fifth segment moderately elongated and the third antennal segment as long as the second, and in these characters it may be excluded from the Aspidiotini and the Odonaspidini.

#### *Second-instar male*

The second-instar males of the four species of *Annonogena* lack marginal appendages except for prominences probably representing trullae. This means that they afford no positive evidence to show the taxonomic position of the genus, because the classification of the Diaspididae is largely based on the marginal appendages. However, they have macroducts of the two-barred type, and this fact excludes the genus from the Aspidiotini. In the undeveloped marginal appendages these second-instar males are comparable to the adult females of the Odonaspidini. The second-instar males of many Odonaspidini, in contrast with the adult females of the tribe and also with the second-instar males of *Annonogena*, are provided with well-developed marginal appendages, of which the pattern shows that the tribe is closely related to the Parlatoriini. The Odonaspidini are associated with Poaceae, usually occurring under the leaf-sheath, and no pupillarial form has been known to occur in the tribe. In all these respects, there seems to be no good reason to refer *Annonogena* to the Odonaspidini. Thus, by means of exclusion, *Annonogena* is referable to the Parlatoriini, if it should belong to any of the established tribes.

In the section Evolutionary changes, *Annonogena* is compared with *Parlatoria proteus*, the type species of *Parlatoria*, and the two known species of the pupillarial genus *Ligaspis*, which definitely belongs to the Parlatoriini. The second-instar males of *Annonogena* are similar to those of *Ligaspis* in the arrangement of the dorsal and ventral macroducts. In the arrangement of the dorsal macroducts these genera do not radically differ from *Parlatoria proteus*. Thus the occurring pattern of macroducts in the second-instar male does not contradict the view that *Annonogena* belongs to the Parlatoriini. As compared with *Parlatoria* and *Ligaspis*, *Annonogena* is characteristic in having slender ducts in most segmental corners of the abdomen; as stated in the generic description, these ducts are usually associated with processes that are interpretable as rudimentary pectinae, whereas the second-instar males of *Parlatoria* and *Ligaspis* have well-developed glanduliferous pectinae.

#### *Adult male*

Several adult males of *A. acutilobata* were obtained from within their tests. (The mounted specimens are not in good condition probably because they were teneral.) They show three of the six characters mentioned by Ghauri (1962) as exclusive to the Parlatoriini: the prescutum is subtriangular rather than transverse or subquadrate; a pair of small setae occur on the lateral sides of the prescutum; and the abdomen is provided with submedian dorsal setae only on the basal three segments. They disagree with Ghauri's concept of the adult male Parlatoriini in the other three characters.

Throughout the family, the genera examined for the adult male are too few to make a conclusive discussion on the higher taxonomic position of *Annonogena* by the use of characters of the adult male.

Further, Ghauri examined the adult male of *Rugaspidiotus tamaricicola*, and recognized the group ‘Diaspidini+Odonaspidini’ on the supposition that the species belongs to the Odonaspidini. In reality, this species, now *Prodiaspis tamaricicola*, is not a member of the Odonaspidini. A comparison of adult male characters based on numerical methods shows the possibility that it forms the nucleus of a separate group (Davies and Boratyński, 1979), whereas a study of the first instar indicates that it belongs to the Diaspidinae and probably to the Diaspidini in accordance with Ghauri’s analysis (but not with his conclusion) (Takagi et al., 1997). In my observations, *Odonaspis* shows a close affinity with the Parlatoriini in the adult male as well as in the first instar and the second-instar male.

#### EVOLUTIONARY CHANGES

In the above section, the pupillarial genus *Annonogena* is referred to the Parlatoriini mainly by means of excluding other possibilities. In fact, there is no positive evidence to support this taxonomic position in the adult female and the second-instar female and male. If this position is correct, the genus should have undergone drastic changes, starting from a form that had an ordinary parlatoriine pattern of characters. In this section, it is compared with *Parlatoria proteus* (Figs 15–18) and the two known species of *Ligaspsis*, *L. maculata* and *L. pala* (Takagi, 2002: Figs 11–17) for examining its evolutionary changes. *P. proteus*, the type species of *Parlatoria*, represents an ordinary non-pupillarial parlatoriine form. *Ligaspsis* is a pupillarial genus, and undoubtedly belongs to the Parlatoriini; it is adopted because figures of the adult females and nymphs of the two species have been published.

Britten and Davidson (1969) proposed a model system for genetic regulation in cell differentiation. This system is built up of intricately overlapping batteries of genes, of which the functions are differentiated hierarchically in accord with the system’s structure, and thus it implies various phenomena of phenotypic changes as its outcomes in development and evolution. In the course of life history, activated batteries of genes should partly and variously differ between the sexes and among the instars. On the other hand, the common occurrence of particular phenotypic characters in different instars, which have different adaptive roles, may be due to batteries of genes activated commonly to those instars, and is termed ‘phenotypic attraction’ in this paper. Such a character, developed adaptively in a particular instar, may primarily have no adaptive significance in the other instars in which it is manifested. In the course of evolution, changes in the organization and activation of batteries of genes will result in such diverse modes as gradualism and saltation, novelty and atavism, and so on. Moreover, ‘The properties of the model regulatory system suggest that *both the rate and the direction of evolution (for example, toward greater or lesser complexity) may be subject to control by natural selection*’ (Britten and Davidson, 1969; their italics). (In their later papers, these authors reviewed the model system with emphasis on experimental information.)

#### *Adult female*

In *Parlatoria*, the pygidium is fringed with well-developed appendages, which are sclerotized trullae and glanduliferous pectinae; the prepygidial abdomen is also provided with marginal appendages, but the trullae are replaced with non-glanduliferous pectinae. In *Ligaspsis*, these appendages are much reduced in size and modified in shape, and confined to the pygidium. In *Annonogena*, there is no trace of marginal



appendages. Protected by a sclerotized exuvial cast of the preceding instar, the adult female of a pupillarial form is no longer engaged in test formation, which requires wax production and, in many forms, pivotal movements of the insect body. In association of this change of behaviour, the pupillarial mode causes reductive changes in external features, especially in wax-secreting organs and marginal appendages. Although it is not well known how the marginal appendages are used in test formation, their complete disappearance in some pupillarial adult females supports the view that they have developed in association with test formation.

In *Parlatoria*, gland tubercles and microducts occur along the margin on the thoracic and basal abdominal segments, and they should be homologous with the glanduliferous pectinae on the succeeding segments. In *Ligaspis*, small ducts occur in a continuous row along the prepygidial margin, apparently corresponding to the prepygidial pectinae, gland tubercles, and marginal microducts in *Parlatoria*. In *Annonogena*, small submarginal ducts occur in the region representing the thoracic and basal abdominal segments, forming segmental groups, and thus correspond to the gland tubercles and marginal microducts occurring on those segments in *Parlatoria*.

*Parlatoria* possesses abundant macroducts marginally and submarginally on the dorsal surface of the abdomen. *Ligaspis* has only two pairs of marginal macroducts on the pygidium, which are apparently much reduced in size. *Annonogena* has no macroducts. Instead, it is usually provided with a variable number of slender ducts on the pygidial margin. As a possibility they may be modified marginal macroducts. In another possibility, they may correspond to pygidial pectinae in *Parlatoria* and *Ligaspis*. The latter possibility is more likely because, in general, gland tubercles, which are homologous with glanduliferous pectinae, are often replaced with microducts.

In *Ligaspis*, the second-instar female and male have the marginal appendages represented fairly well and the macroducts not reduced in size and, in the male, rather abundant, in spite of the remarkably reductive changes of these features in the adult female. Apparently, the batteries of genes responsible for these features are not lost in the genome and only inactivated in the adult female, and this may be generalized for other pupillarial genera.

The adult females of *Annonogena acutilobata* and *A. rotundilobata* show an irregularly undulate or reticulate linear pattern on the dorsal margin of the pygidium. Such patterns are unknown in *Parlatoria* and *Ligaspis*. The second-instar females of *Annonogena*, however, have corresponding patterns: in all the four species, the dorsal disc shows a reticulate sclerotized pattern on a narrow or broad marginal area. It seems as if the reticulate pattern on the nymphal derm were printed negatively on the adult derm, nearly entirely in *A. rotundilobata* and partially in *A. acutilobata*. (Only an obscure pattern has been observed in the adult female of *A. echinata*; no trace of such a pattern has been found in *A. aristata*, in which, however, no good specimens of the adult female have been available). If the linear pattern in the adult female really corresponds to the reticulate pattern in the second-instar female, the manifestation of the former may be attributed to phenotypic attraction on the supposition that the reticulate pattern developed adaptively in the second-instar female.

#### *First instar*

The first-instar female and male of *Parlatoria proteus* are provided around the pygidial apex with a set of marginal appendages, which are composed of strongly

sclerotized robust trullae and well-fimbriate pectinae. In the first-instar nymphs of *Ligaspis maculata*, *L. pala*, and *Annonogena acutilobata*, the corresponding appendages are much reduced in size and simplified in shape: the trullae are modified into slender processes and the pectinae are also modified into slender processes or practically obsolete. These nymphs differ also in several other features, in which, however, even *Ligaspis maculata* and *L. pala* are not exactly the same, and such differences may be no more than specific. In the Diaspididae, in principle, the marginal appendages are commonly possessed by the nymphal instars and the adult female. The view is adopted that they have developed in association with test formation. In the diaspidid life history, the adult female has the leading role in test formation and, thus, it should be the driving stage in the evolution of these appendages. On the other hand, the second-instar females and adult females of various genera and the heteromorphic second-instar males of some Diaspidini have the marginal appendages much reduced or obsolete, and yet form good tests. Marginal appendages, therefore, are not indispensable for test formation under some conditions. This fact suggests that the possession of well-developed appendages does not always mean their utility. The problem here is whether the marginal appendages in the first instar have any role. Their state in the pupillarial genera *Ligaspis* and *Annonogena* in contrast to that in *Parlatoria* admits the possibility that the marginal appendages even if well developed have no role in the first instar and their occurrence in this stage is due to phenotypic attraction, thus reflecting the state in the conspecific adult female.

#### *Second-instar male*

The second-instar nymphs of both sexes in *Ligaspis* are provided with marginal appendages occurring in a continuous series on the pygidium, and these appendages demonstrate a close affinity with those in non-pupillarial Parlatoriini. However, when the state in the second instar of *Parlatoria proteus* is adopted as the standard, these appendages in *Ligaspis* are not fully formed: the trullae are modified into angular processes and the pectinae are less fimbriate. They may have little function: the second-instar female forms no appreciable test and the completed male test is parallel-sided and thus suggests no pivotal movement of the insect body in test formation. In *Annonogena* the reduction of the marginal appendages is nearly complete in the second-instar male, which constructs an elongate, parallel-sided test.

A remarkable character in the second-instar males of *Annonogena* and *Ligaspis*, as compared with *Parlatoria*, is the occurrence of macroducts on both the dorsal surface and the ventral surface of the abdomen. This amphisomatic occurrence of macroducts is known also in the second-instar males of other various taxa. It is unusual in the adult female and the second-instar female, but has been observed in the adult female and the second-instar female and male of *Amphisoma erectum* (Diaspidini, Diaspidinae), and in the adult female and the second-instar female of *Galeomytilus obesus* (Lepidosaphidini, Diaspidinae) (Takagi, 1995). The second-instar male of *G. obesus* has not been examined, but it is quite possible that it also possesses ventral macroducts. In these species it is easy to interpret the adaptive significance of the amphisomatic occurrence of macroducts: both the females and the males of these species inhabit the hirsute parts of the host plant (*Colona serratifolia*), standing on the anterior end of the body among the dense erect hairs of the plant, and thus construct standing tests with the ventral portion formed well like the dorsal.

It is reasonable to suppose a relatively undifferentiated state between the dorsal and ventral surfaces to be primitive as compared with a well-differentiated state. The amphisomatic occurrence of macroducts in *Amphisoma* and *Galeomytilus*, therefore, may involve atavism, and it is apparently adaptive. The significance of the amphisomatic occurrence of macroducts in the second-instar males of the other taxa including *Annonogena* and *Ligaspis* is not clear. In a considerable part of the family, especially in many species belonging to the Diaspidini (Diaspidinae) and the Odonaspidini and Smilacicolini (Aspidiotinae), the heteromorphic second-instar males are apparently primitive or atavistic as compared with the second-instar and adult females. This phenomenon, not restricted to a particular group, should arise from a genetic background that is universal in the family. The amphisomatic occurrence of macroducts in the second-instar male may reflect such a background.

#### *Second-instar female*

The differences in this stage between *Annonogena* and *Parlatoria* or *Ligaspis* are so great that it is not possible to attribute them to reduction or other ordinary changes. Above all, the second-instar females of *Annonogena* bear unusual or unique features: the operculum, dorsal lobules, ventral lobules, and the perforated flap.

As stated, the occurrence of an operculum on the exuvial cast of the second-instar female, though unusual in the Diaspididae, is not unique to *Annonogena*. The family Halimococcidae, composed exclusively of operculum-bearing pupillarial forms, is interpreted as a primitive relative of the Diaspididae on the basis of the first instar (Takagi et al., 1997). If their close relationship means that they have in common many active and dormant batteries of genes including those concerned with the formation of the operculum, the sporadic occurrence of operculum-bearing pupillarial forms in the Diaspididae is not unexpected. In *Annonogena*, the operculum is transversely sulcate basally and reticulate marginally, and this pattern of sclerotization seems to be effective in reinforcing the operculum, which is a hinged lid.

The usual marginal appendages of the Aspidiotinae, the trullae and pectinae, are formed by extensions of the ventral surface of the body. It is not difficult to suppose that the ventral lobules of *Annonogena* are modifications of the usual trullae and pectinae. If the perforated flap is also homologous with the usual marginal appendages, it should represent a primordial state of the latter. On this understanding, the ventral lobules should develop from the perforated flap through a process involving apoptosis along the rows of perforations.

The dorsal lobules in *Annonogena acutilobata* and *A. rotundilobata* occur along the margin of the dorsal disc or the operculum, and therefore cannot be homologous with the usual marginal appendages, which are ventral in origin. It is apparent by the use of the marginal setae on the operculum as landmarks that the dorsal lobules in these species correspond to the marginal sclerites in *A. echinata* and *A. aristata*. The dorsal lobules therefore should be extended marginal sclerites. They are smaller than the ventral lobules but similar to the latter in shape. The question arises why the dorsal lobules are so similar to the ventral lobules in spite of their different origins. A possible explanation may be found in their location on the pygidial margin, where the dorsal and ventral surfaces meet, probably with some batteries of genes commonly activated. Under this supposed condition, the marginal sclerites should extend to take the shape of lobules in concert with the formation of the ventral lobules.

In pupillarial diaspidids, the marginal appendages may completely disappear in the adult female, and may be more or less reductive in the nymphs owing to phenotypic attraction. In *Annonogena*, the marginal appendages are nearly completely lost in the males of the second instar, and such a state may be expected for the females of the same instar. In the second-instar females of this genus, however, another extension of the ventral derm, the perforated flap, arises in the place of trullae and pectinae and then, according to the explanation offered above, it divides and develops into the ventral lobules, with the concerted extension of the marginal sclerites into the dorsal lobules. This explanation demands further explanation.

In *A. echinata* a number of spinous processes occur in the prepygidial region of the second-instar female, whereas no traces of such processes are found in the other species of the genus and ordinary parlatoriine forms. It is unknown whether this unusual feature has any adaptive significance but, as a possibility, it may primarily be an overgrowth resulted from the advanced pupillarial mode of life, which requires an overall heavy sclerotization of the derm in the second-instar female. The development of the extraordinary marginal structures of the pygidium in the second-instar females of the *Annonogena* species may also be attributed to overgrowth. While the perforated flap and the ventral lobules may be homologous with the trullae and pectinae, representing a primordial or modified state of the latter, the spinous processes on the prepygidial derm and the dorsal lobules on the pygidium should be novel features in the genus.

In another pupillarial diaspidid, *Suturaspis crataegi* (= *Leucaspidopsis crataegi* Bodenheimer), Leucaspidini, the second-instar females are often equipped with a pair of 'flabella' (each composed of prominent spinous processes connected to form a fan-like structure) on the ventral surface of the pygidium (Fig. 19). Because this structure finds no corresponding feature in the other known diaspidids including the other species of *Suturaspis*, it is assumed to be a novel conformation that has abruptly appeared in *S. crataegi* (Takagi and Moghaddam, 2005).

#### *Concluding remarks*

The extraordinary pupillarial genus *Annonogena* is referred to the Parlatoriini in spite of the absence of positive evidence for this taxonomic position, which is naturally open to question. Probable evolutionary changes from an ordinary parlatoriine form to the genus are discussed, partly with the aid of the Britten-Davidson model, which implies a broad range of phenotypic changes in development and evolution. The interpretations thus attempted, though highly speculative especially as to the operculum, perforated flap and the dorsal and ventral lobules, show how the character patterns of the adult female and nymphs of *Annonogena* are derivable from those of ordinary Parlatoriini.

A question remains: why should *Annonogena* be referred to the tribe Parlatoriini, even if it really originated from a form that undoubtedly belonged to the tribe? The problem may concern the pupillarial mode of life. Many pupillarial genera are known, and their features in the adult females are reductive in various ways and various degrees. The pupillarial genus *Ligaspsis* exhibits an unmistakable parlatoriine pattern in the second instar, but the marginal appendages in this stage as compared with those in *Parlatoria* show apparently reductive changes. Phenotypic attraction, thus, may change nymphal characters in pupillarial genera, and the change may reach such an extreme that few traces of the ancestral non-pupillarial forms are recognizable. In short, pupillarial genera are more or less degenerative phenotypically in the adult female and nymphs (except

for the heavy development of the exuvial cast of the second-instar female). They may not be worthy of new higher taxa, however different they appear from their related non-pupillarial genera. Nevertheless, if the reasoning adopted in the preceding section is not radically wrong, novel structures can appear, though probably rarely, on pupillarial forms. The point here may be whether such a novel structure acquires any critical role in adaptation, causing associated phenotypic changes, and leads up to the emergence of a novel pattern of characters, which means the emergence of a new higher taxon.

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#### CORRECTIONS

Takagi, 2002, mentioned in References above.

p. 57, line 9 from bottom: for 'THREE' read 'TWO'

p. 71, line 2 from top: for 'angiospermes' read 'angiosperms'



Fig. 1. *Annonogena acutilobata*, adult female: B, antenna; C, pygidial margin, dorsal surface; D, pygidial margin, ventral surface. Scale bars: A, 100 $\mu$ m; B–D, 10 $\mu$ m.



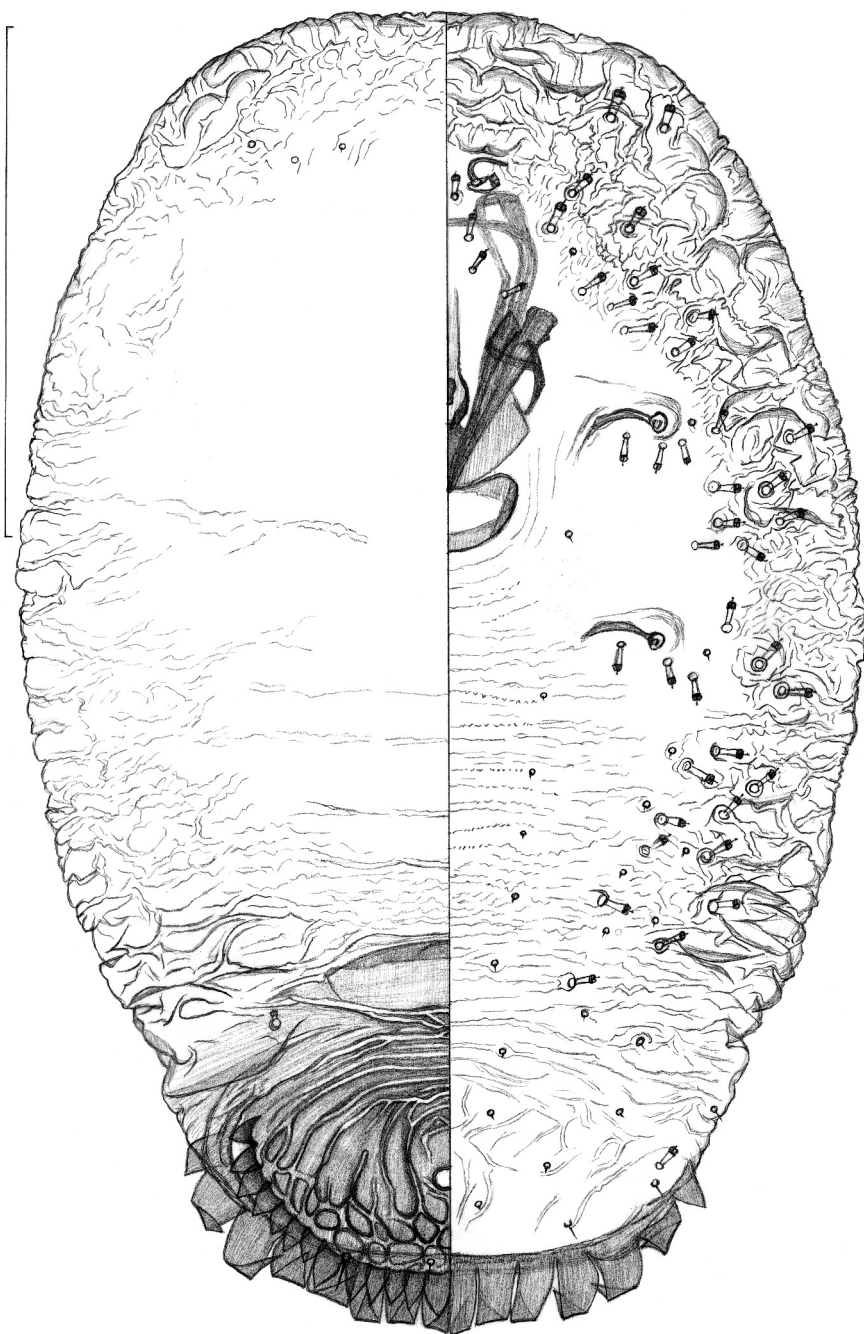


Fig. 2. *Annonogena acutilobata*, second-instar female. Scale bar: 100 $\mu$ m.

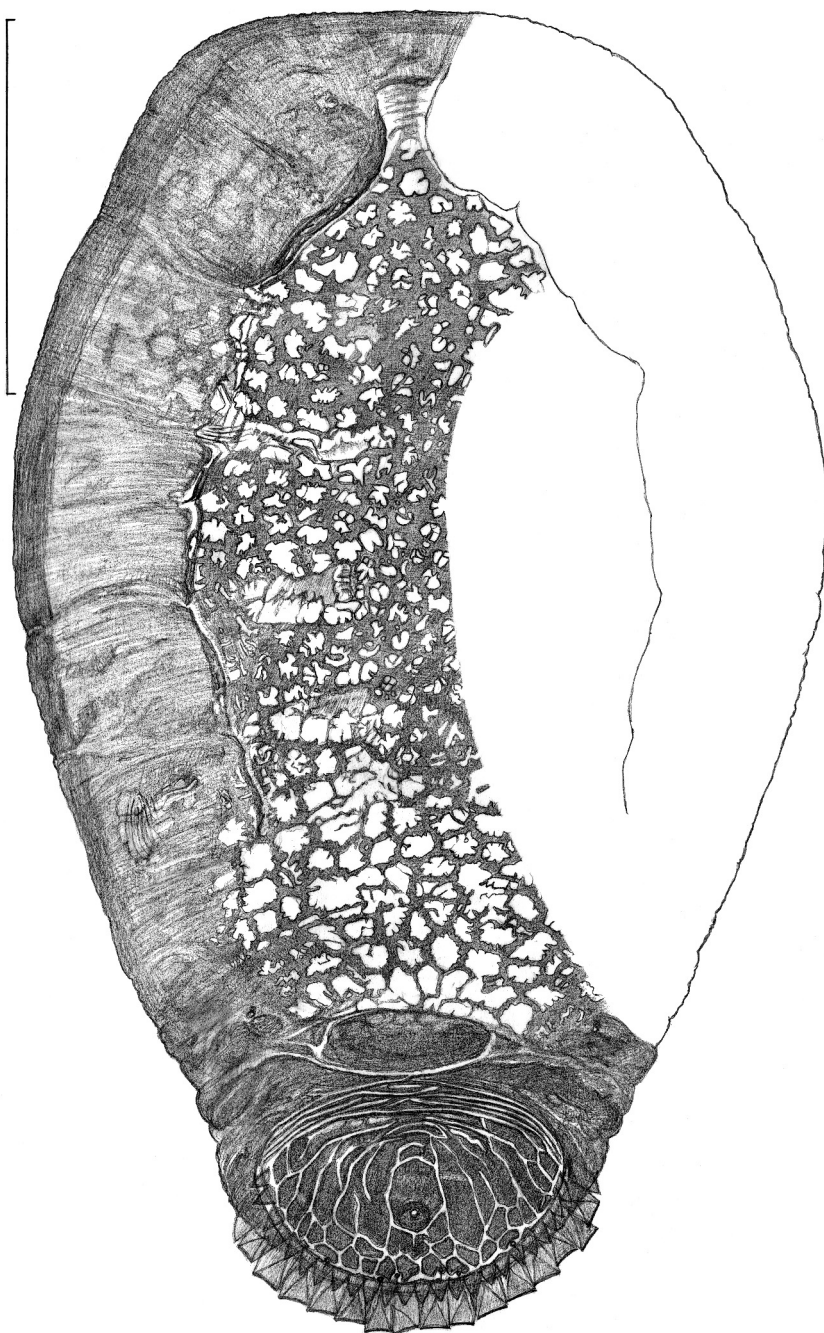


Fig. 3. *Annonogena acutilobata*, exuvial cast of second-instar female. Scale bar: 100 $\mu$ m.



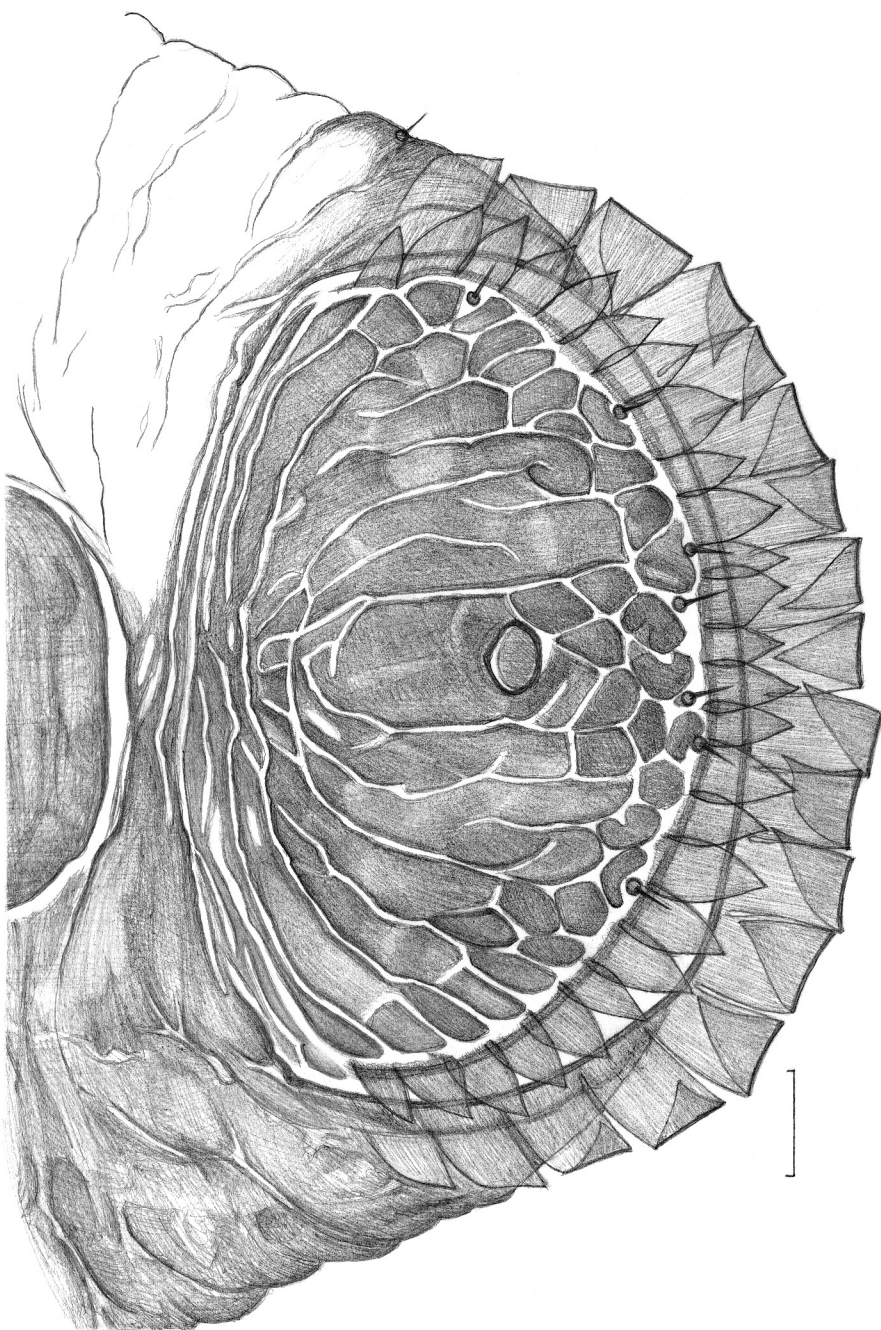


Fig. 4. *Annonogena acutilobata*, exuvial cast of second-instar female: pygidium, dorsal view. Scale bar: 10 $\mu$ m.

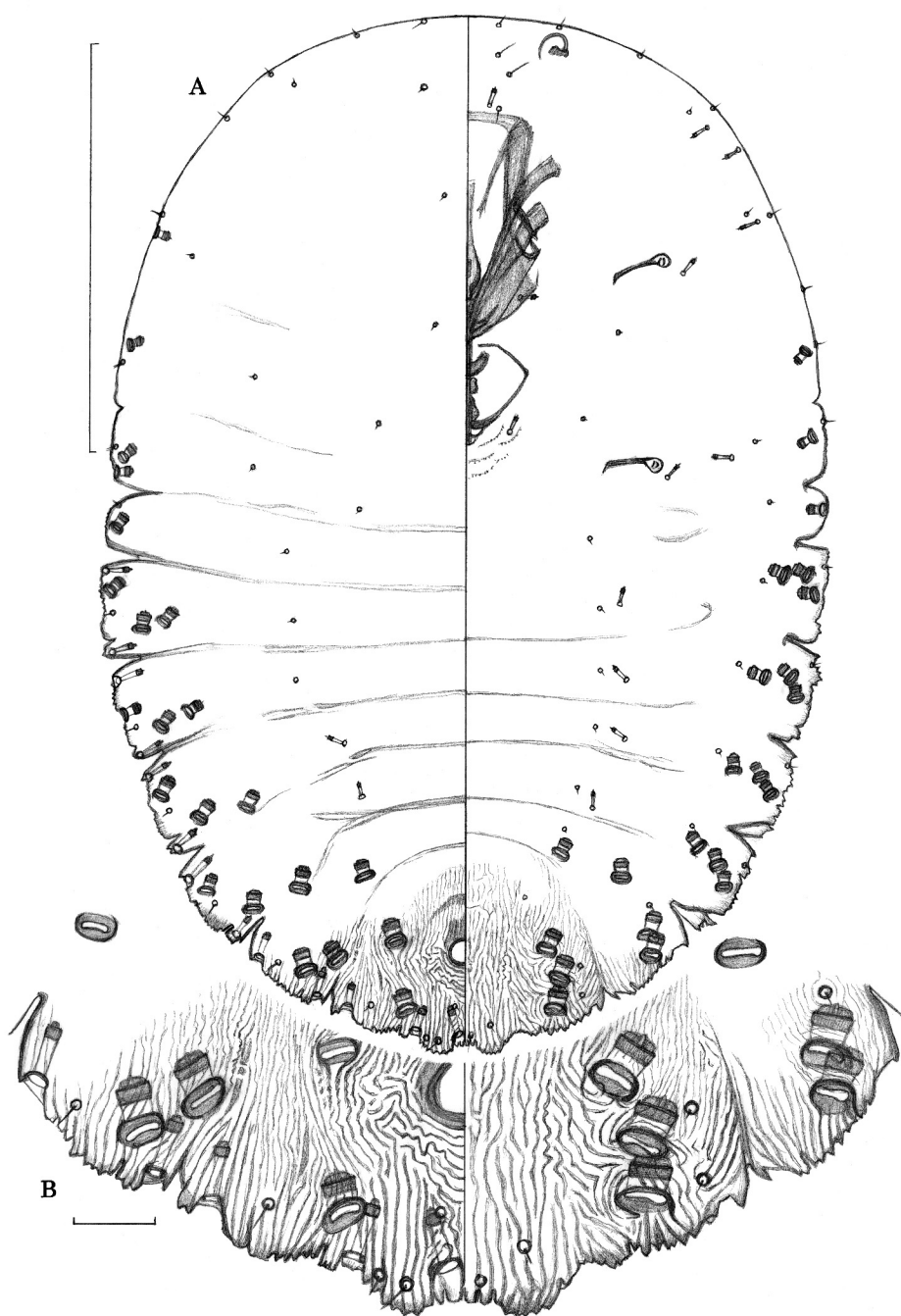


Fig. 5. *Annonogena acutilobata*, second-instar male: B, pygidial margin. Scale bars: A, 100 $\mu$ m; B, 10 $\mu$ m.

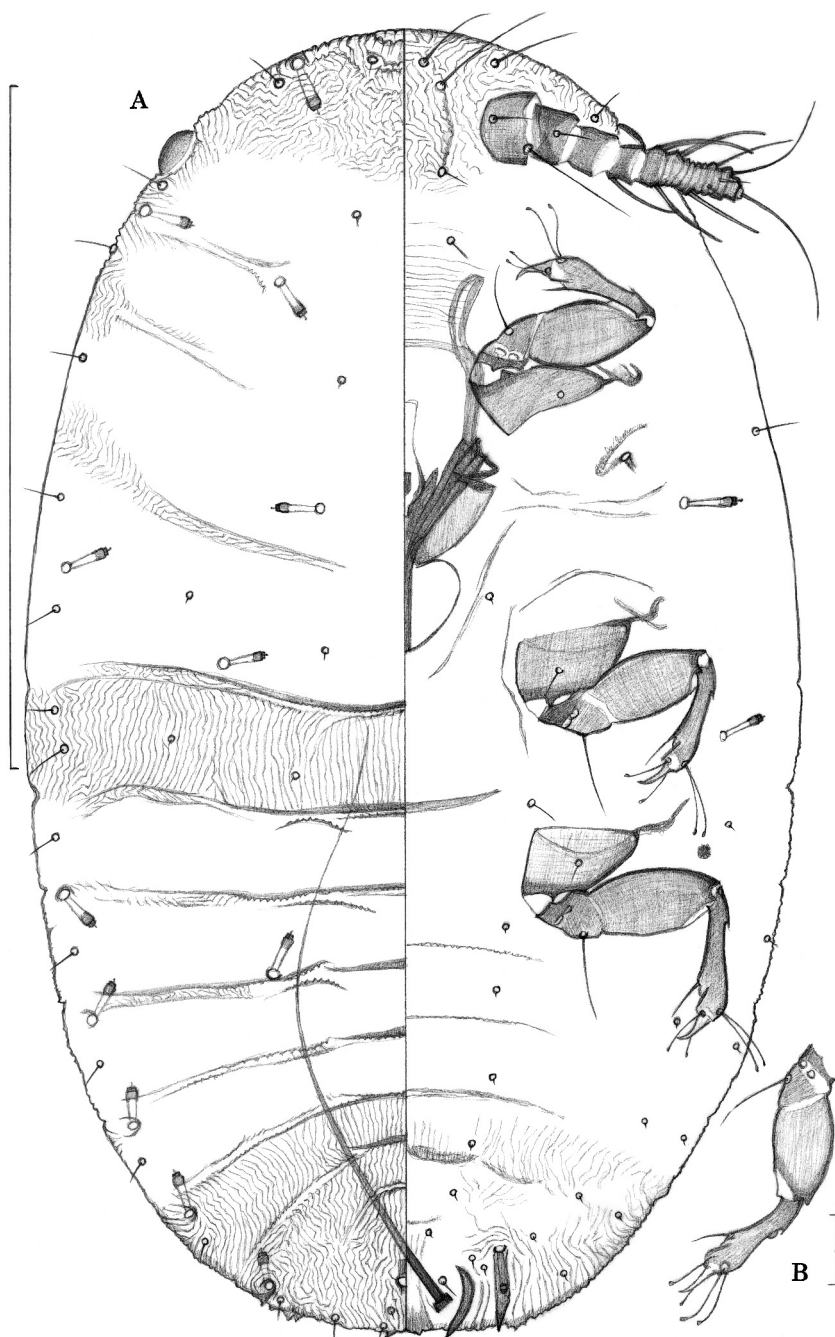


Fig. 6. *Annonogena acutilobata*: A, first-instar female; B, first-instar male, mesothoracic leg. Scale bars: A, 100 $\mu$ m; B, 10 $\mu$ m. The male differs from the female in having a campaniform sensillum on each tibiotarsus and a submedian dorsal seta on each of the first, second, and third abdominal segments.



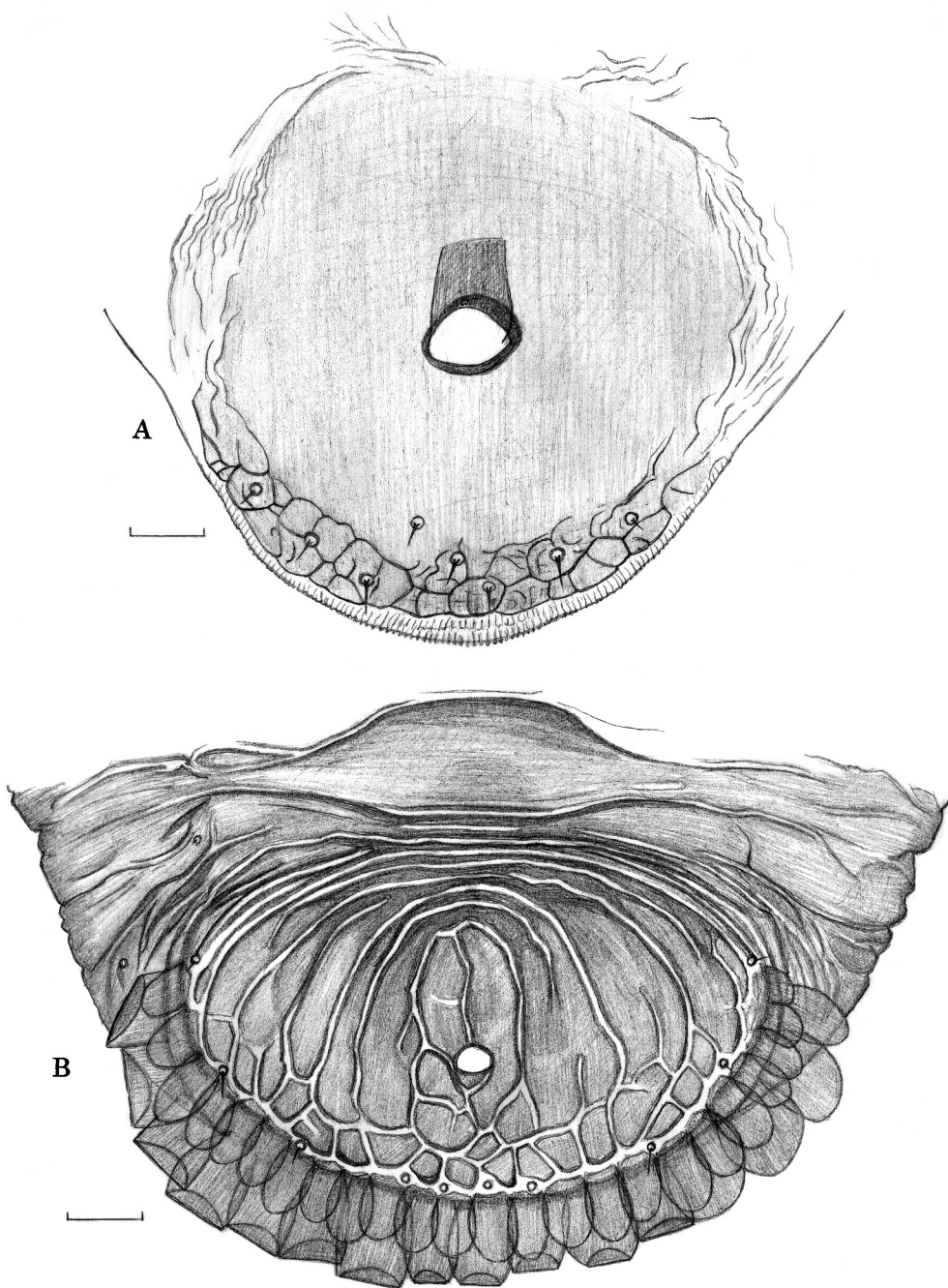


Fig. 7. *Annonogena rotundilobata*: A, adult female, pygidium in dorsal view; B, exuvial cast of second-instar female, pygidium in dorsal view. Scale bars: 10 $\mu$ m.

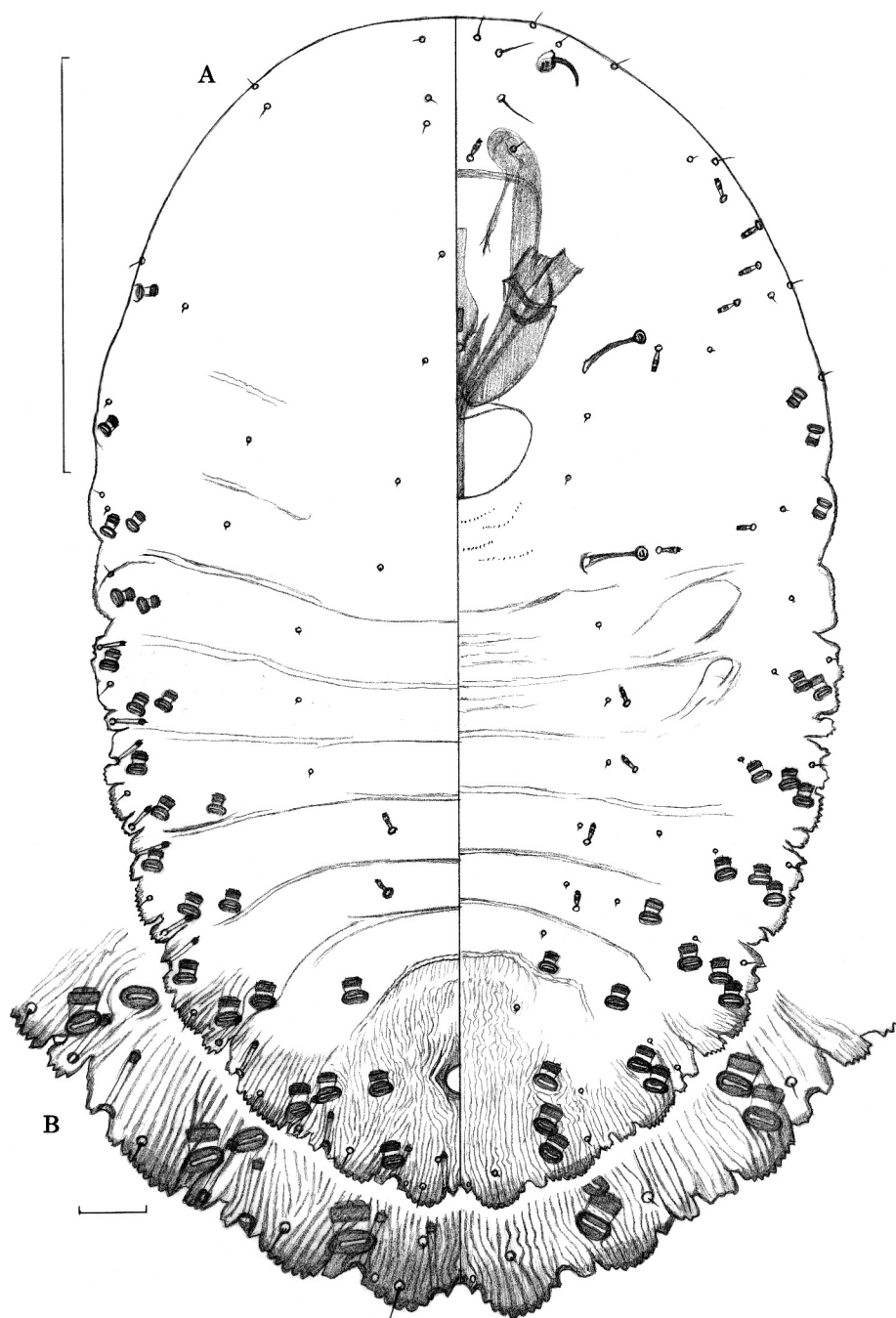


Fig. 8. *Annonogena rotundilobata*, second-instar male: B, pygidial margin. Scale bars: A, 100 $\mu$ m; B, 10 $\mu$ m.

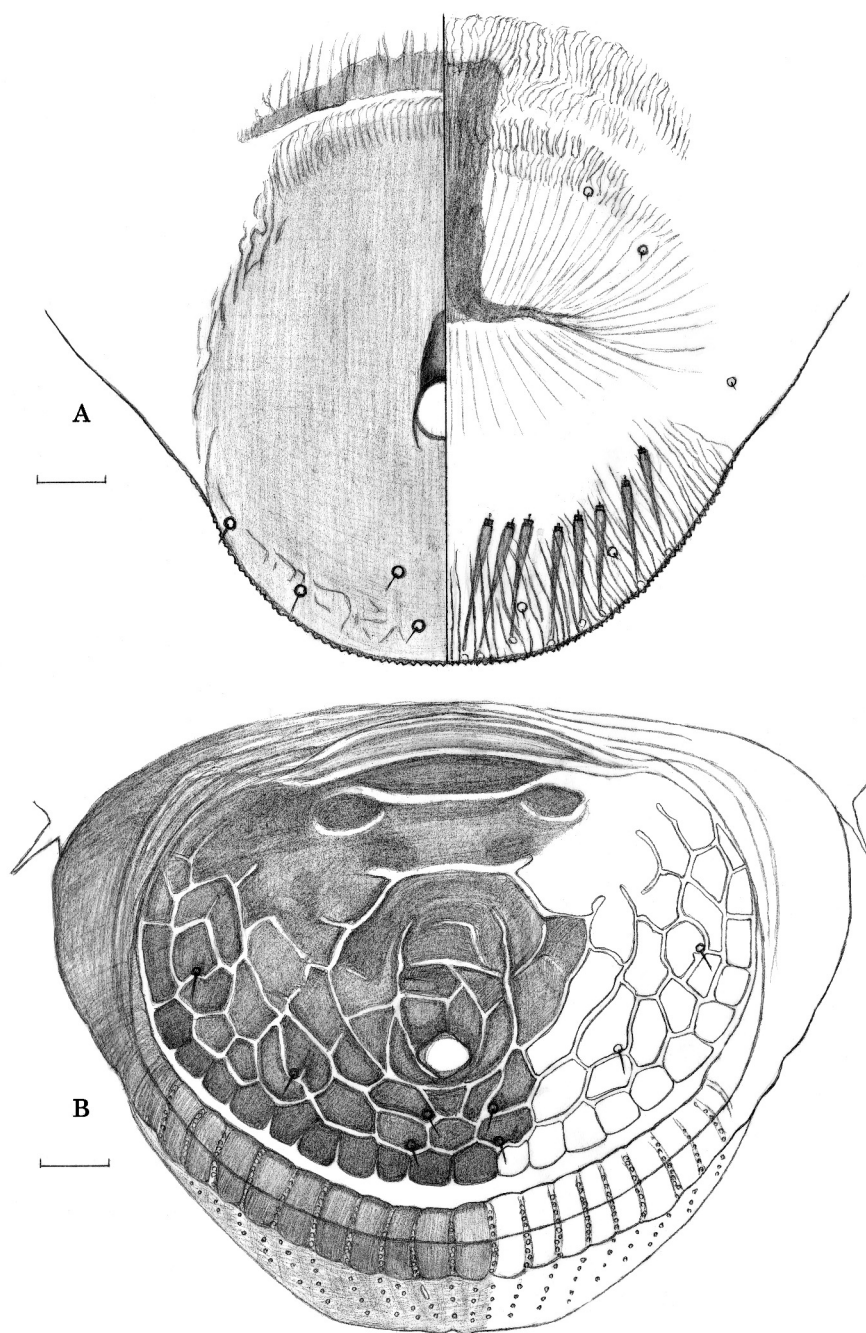


Fig. 9. *Annonogena echinata*: A, adult female, pygidium; B, exuvial cast of second-instar female, pygidium in dorsal view. Scale bars: 10 $\mu$ m.



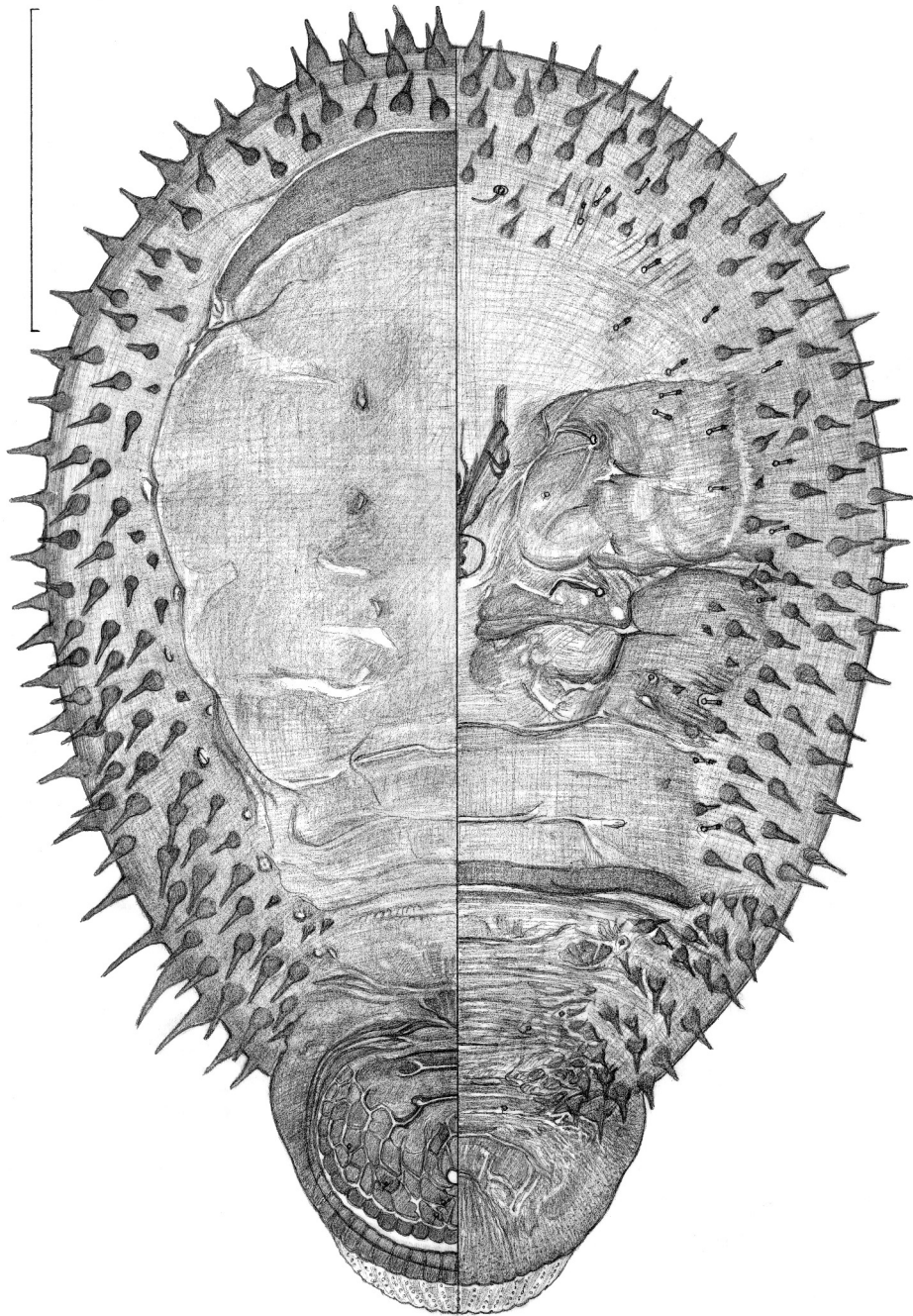


Fig. 10. *Annonogena echinata*, exuvial cast of second-instar female. Scale bar: 100 $\mu$ m.

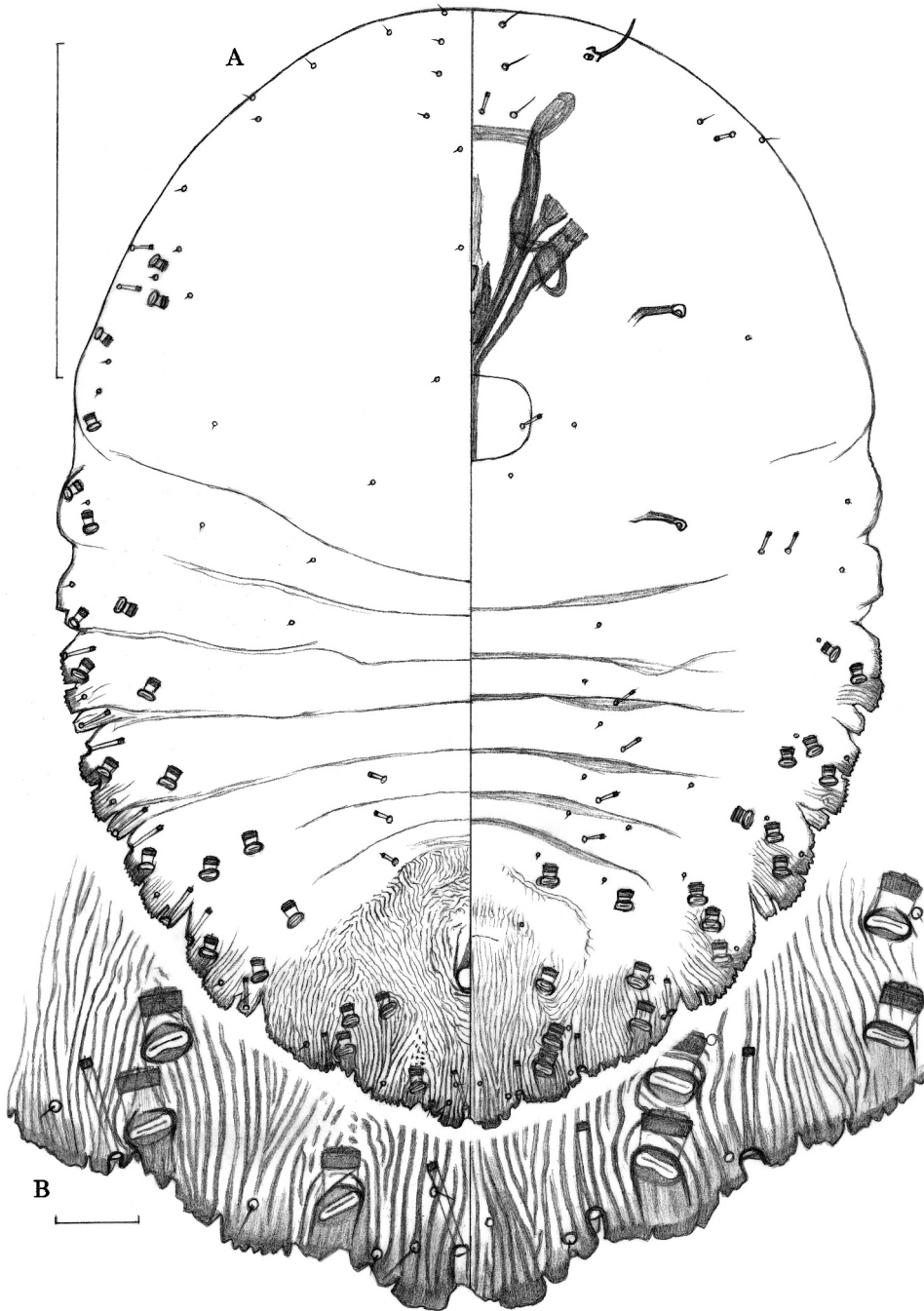


Fig. 11. *Annonogena echinata*, second-instar male: B, pygidial margin. Scale bars: A, 100µm; B, 10µm.



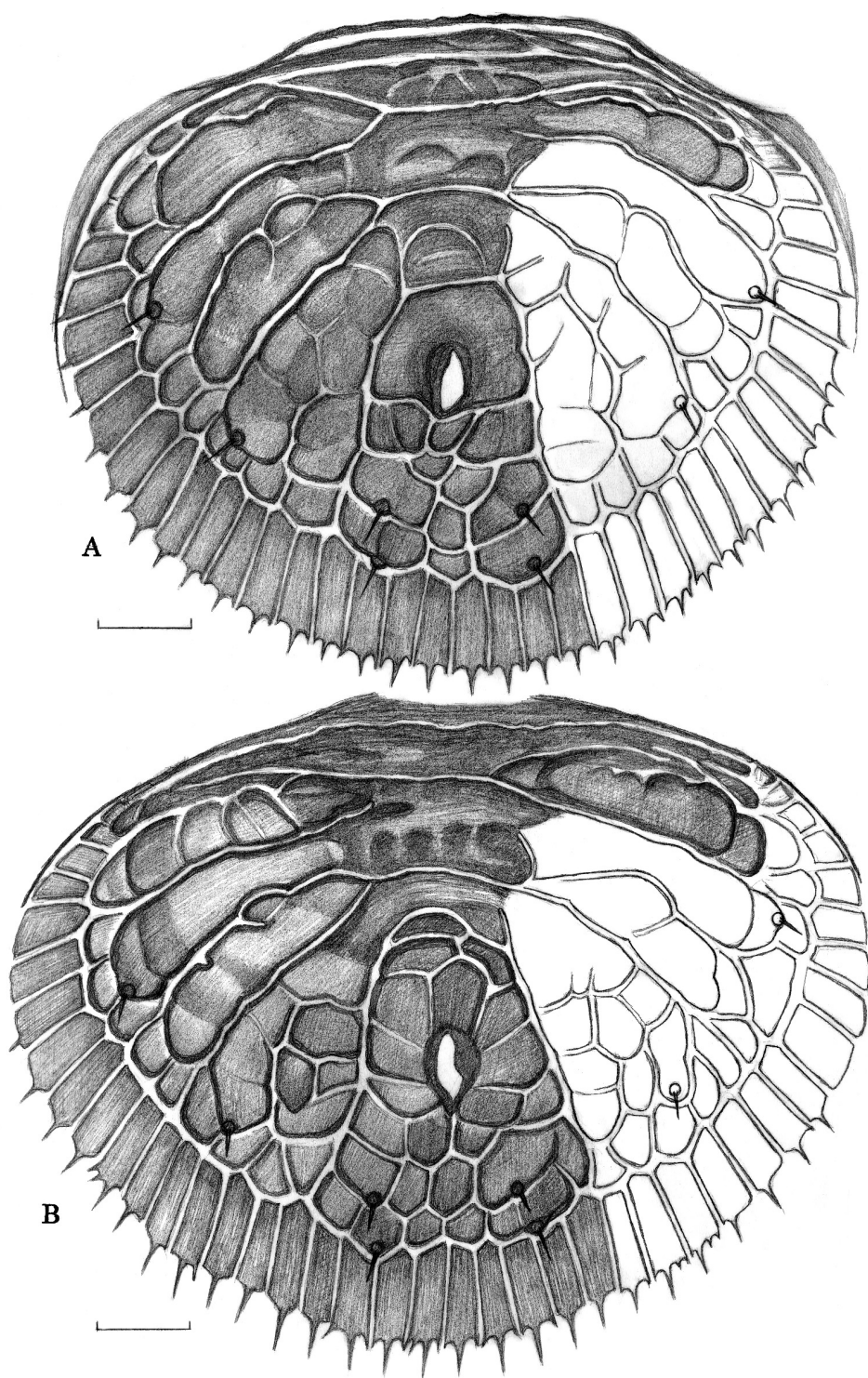


Fig. 12. *Annonogena aristata*: A and B, exuvial casts of second-instar female, operculi. Scale bars: 10 $\mu$ m.

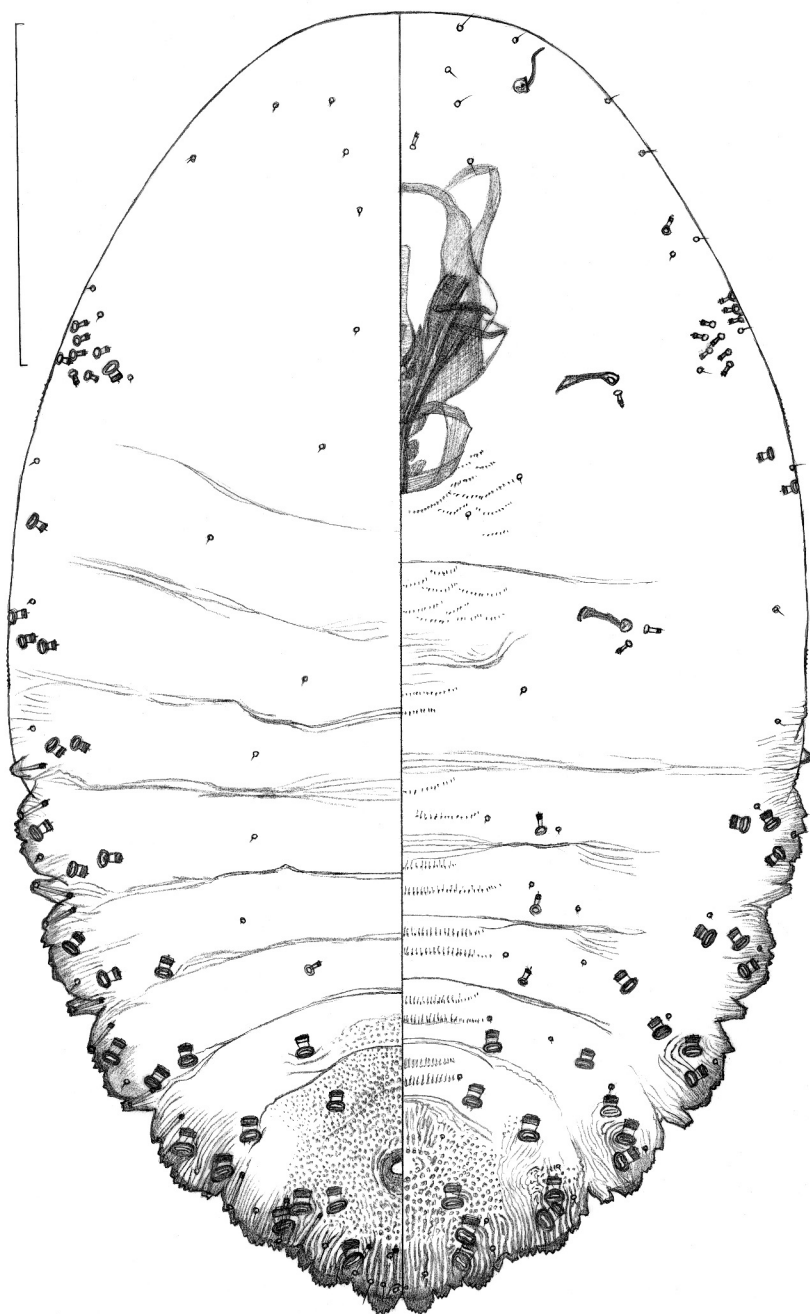


Fig. 13. *Annonogena aristata*, second-instar male. Scale bar: 100 $\mu$ m.

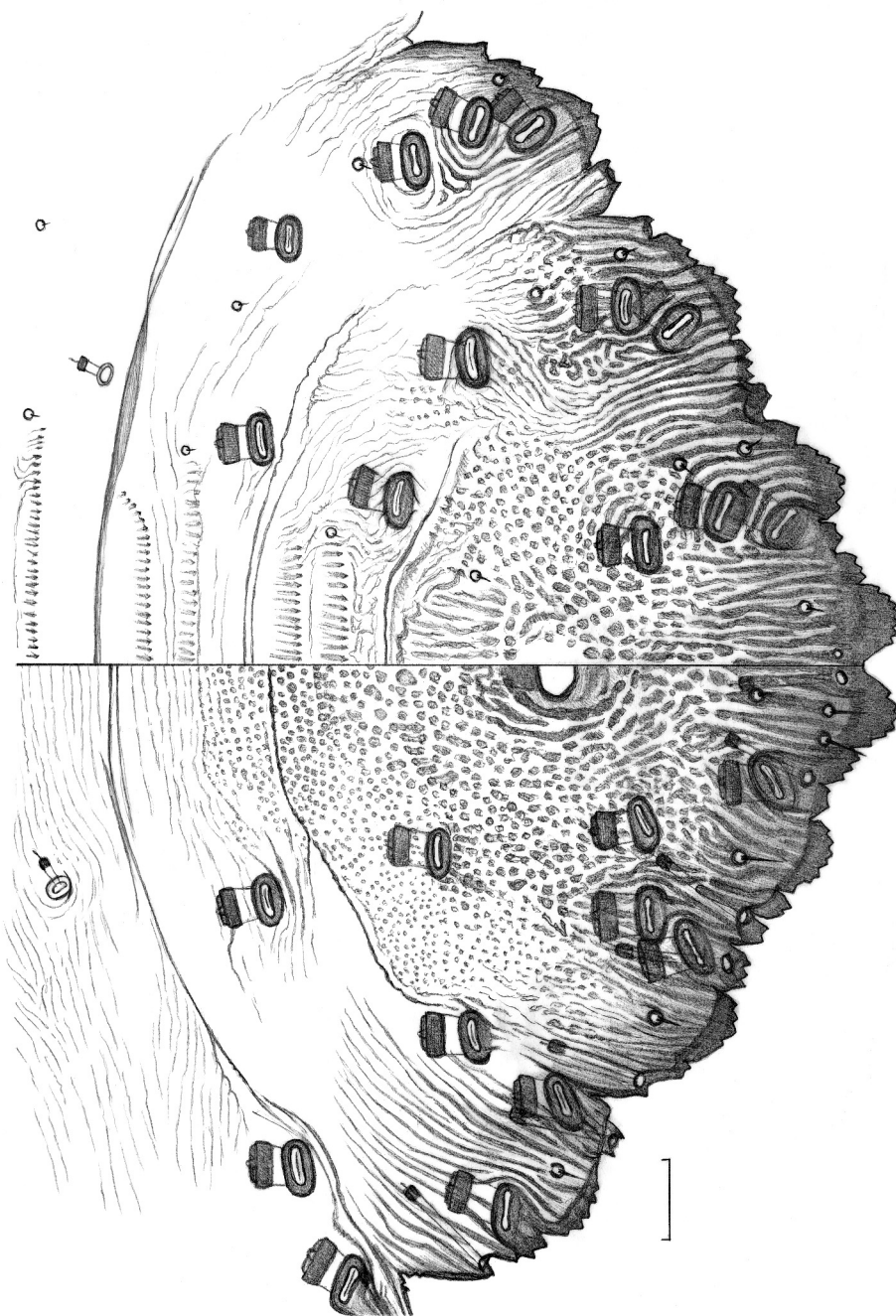


Fig. 14. *Annonogena aristata*, second-instar male, pygidium. Scale bar: 10 $\mu$ m.



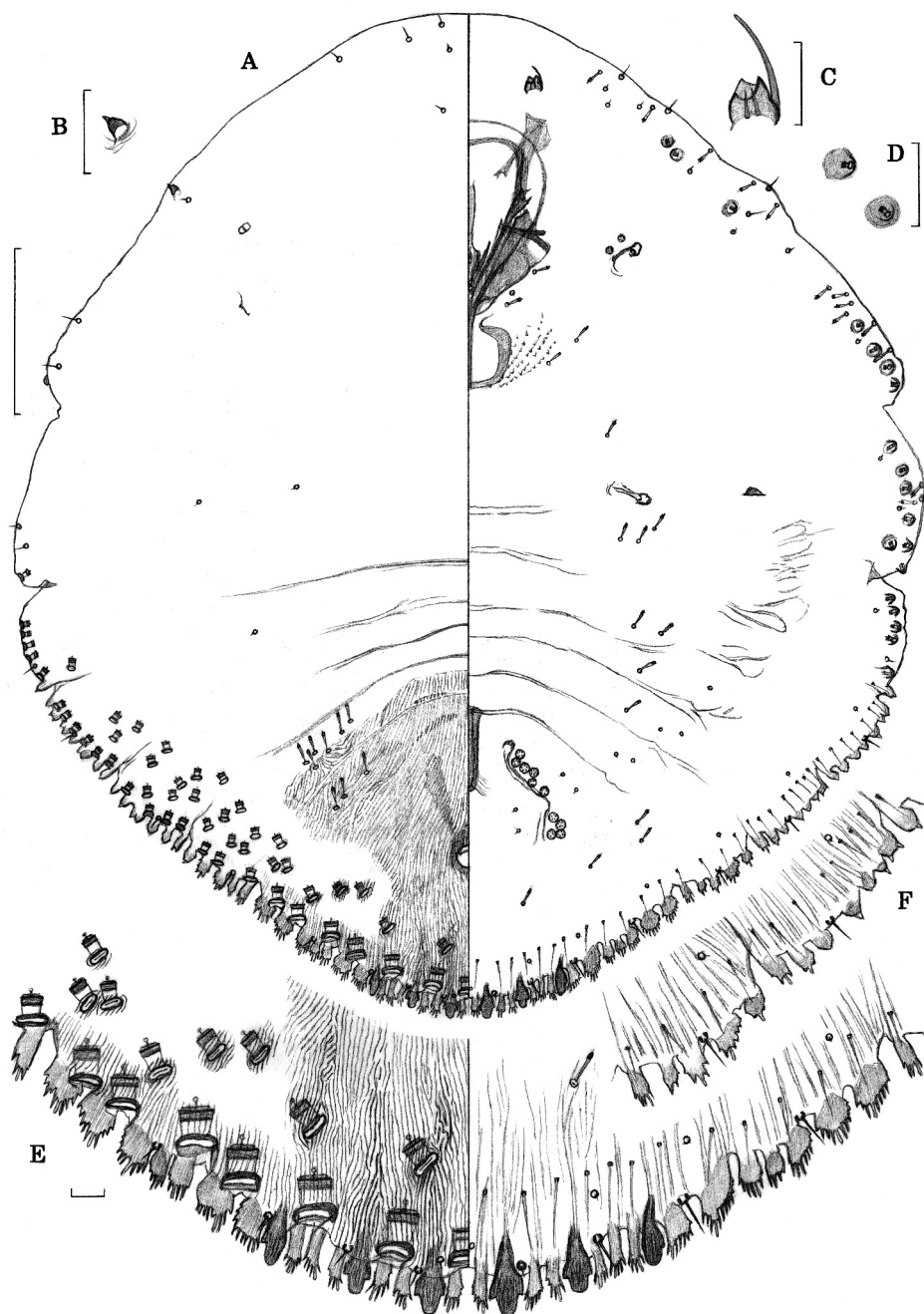


Fig. 15. *Parlatoria proteus*, adult female: B, eye-spot; C, antenna; D, gland tubercles; E, pygidial margin; F, abd III and IV, margin in ventral view. Scale bars: A, 100µm; B–E, 10µm (E and F magnified at the same rate). Figured from a specimen mounted from material collected at Miyazaki, Kyûsyû, Japan, on a slipper orchid under glass, 1957 [57Myz-cyp].

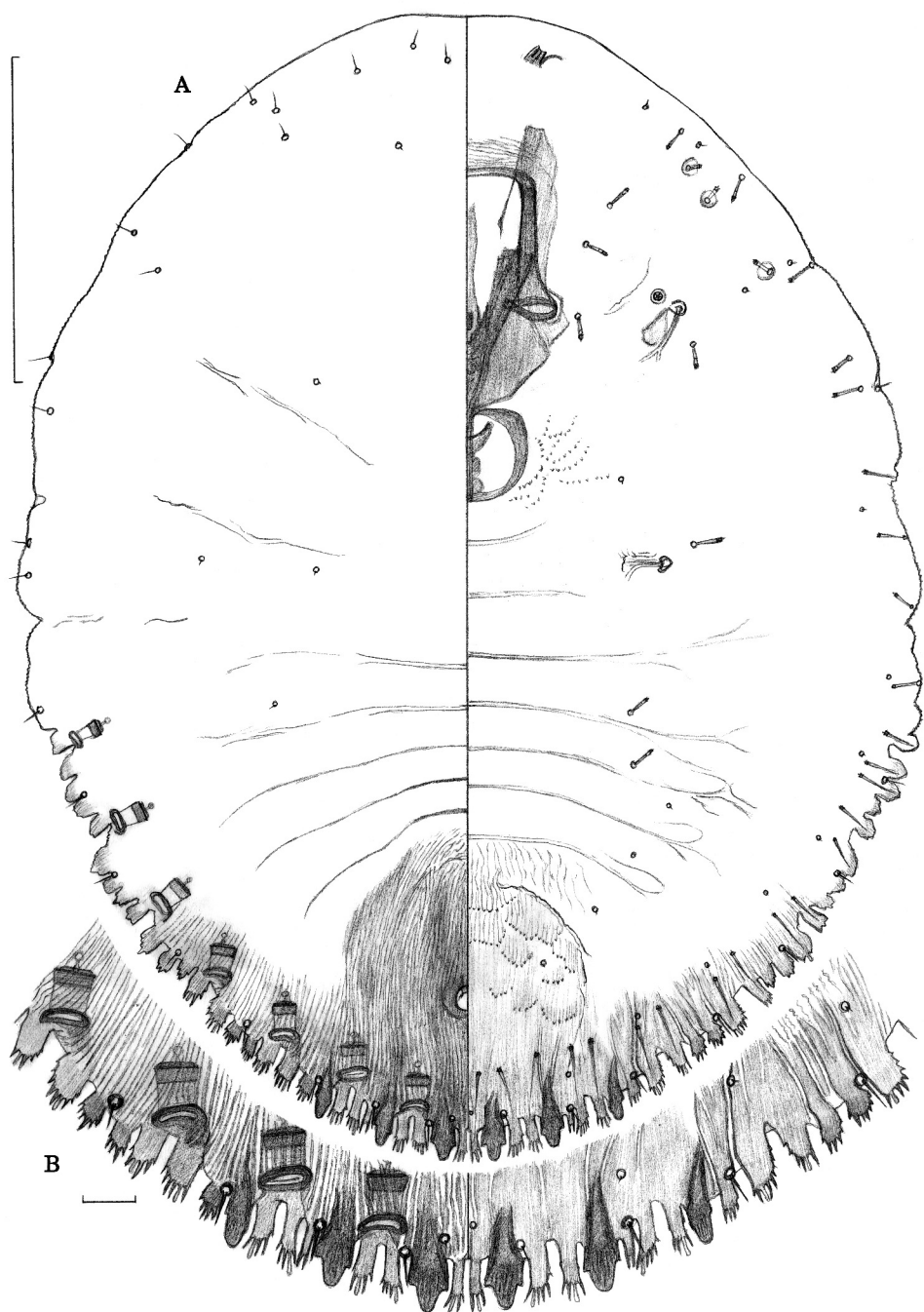


Fig. 16. *Parlatoria proteus*, second-instar female: B, pygidial margin. Scale bars: A, 100 $\mu$ m; B, 10  $\mu$ m. [57Myz-cyp].

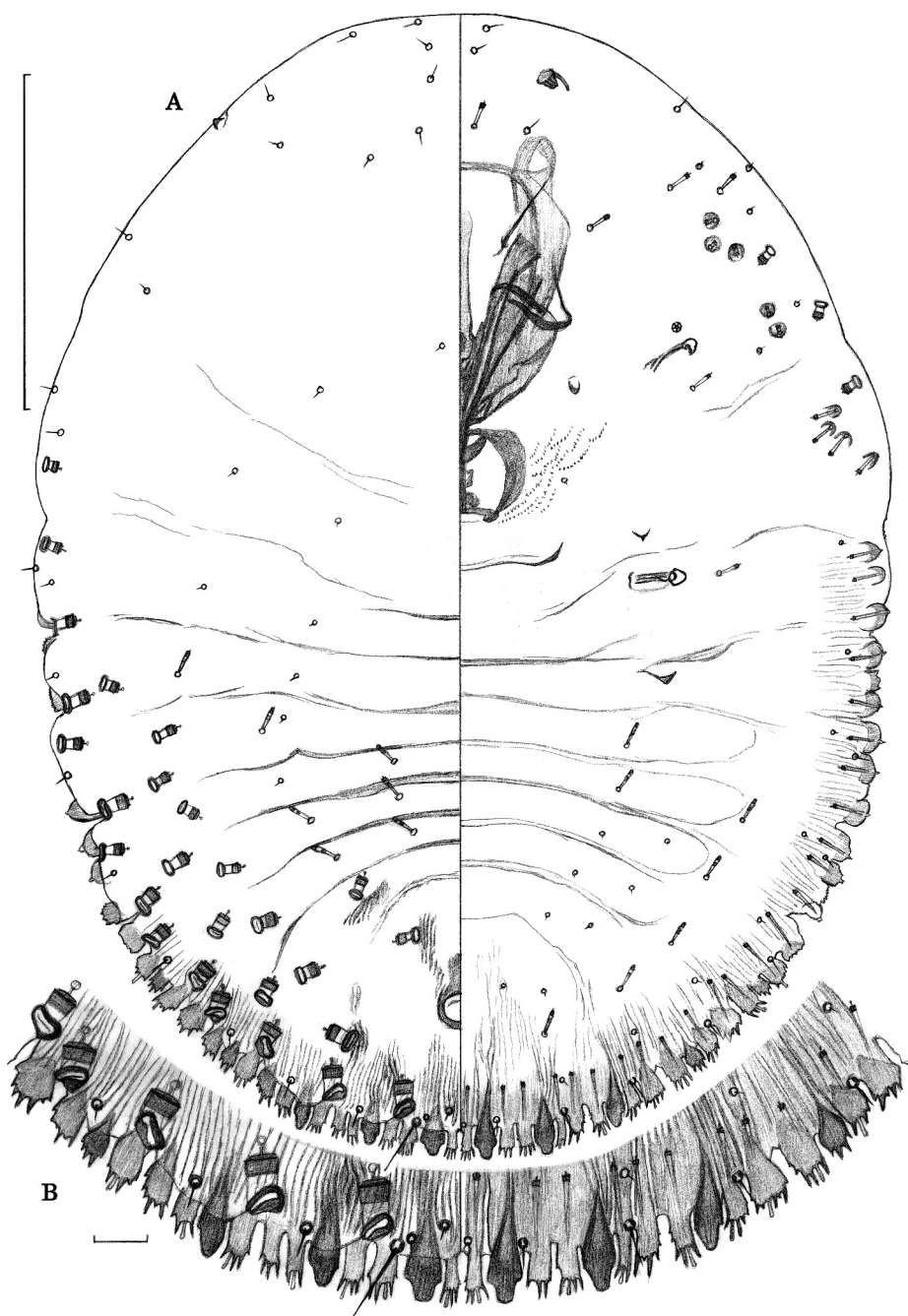


Fig. 17. *Parlatoria proteus*, second-instar male: B, pygidial margin. Scale bars: A, 100μm; B, 10μm. [57Myz-cyp].

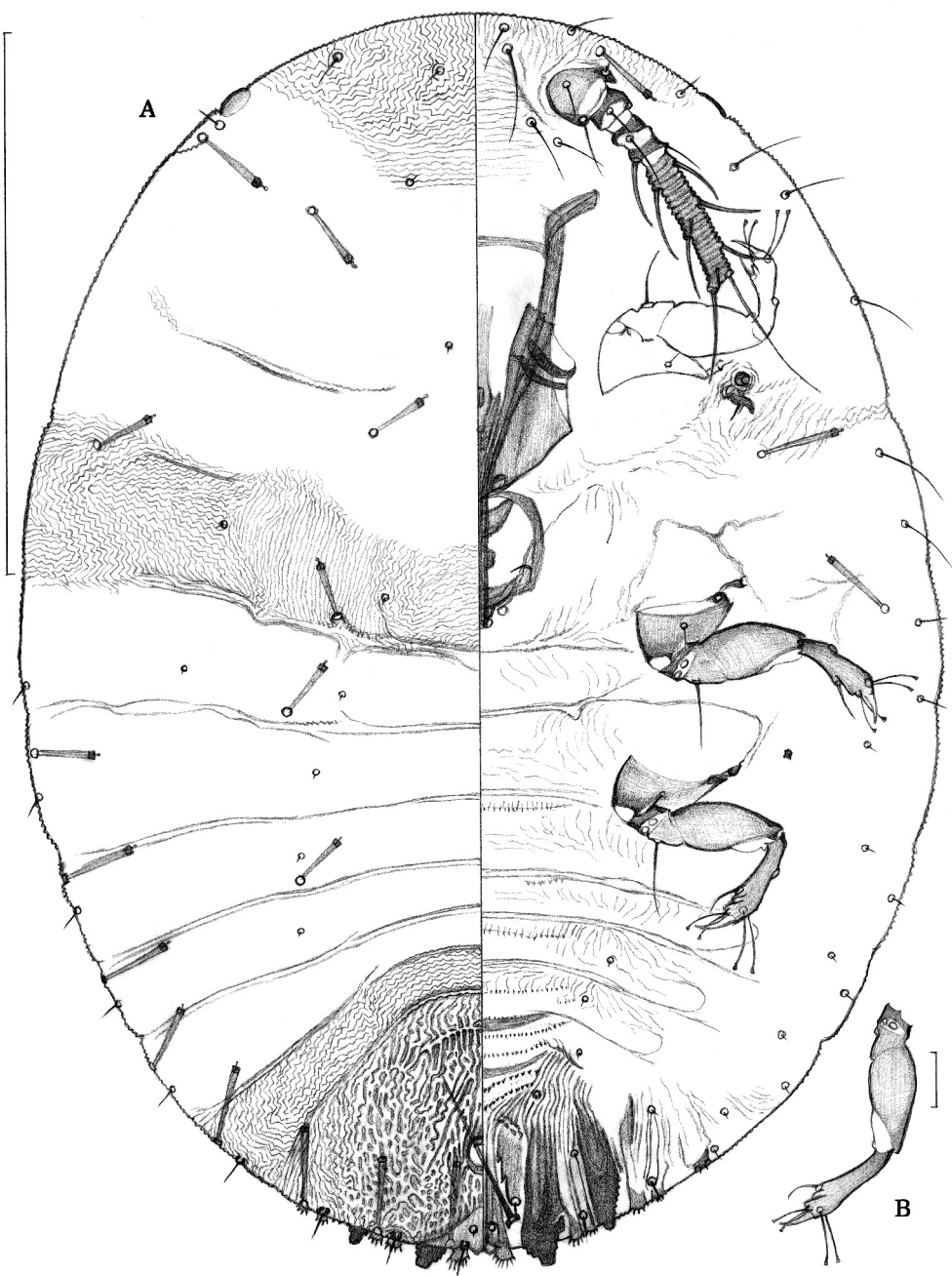


Fig. 18. *Parlatoria proteus*, first-instar nymphs: A, male; B, female, metathoracic leg. Scale bars: A, 100 $\mu$ m; B, 10 $\mu$ m. [57Myz-cyp]. The female differs from the male in having no campaniform sensillum on the legs and no submedian dorsal seta on the first and third abdominal segments.





Fig. 19. *Suturaspis crataegi*, second-instar female: pygidia and flabella, D–F, exuvial casts. Scale bar: 10 $\mu$ m (all magnified at the same rate). Iran, on *Daphne angustifolia*. (Reproduced from Takagi and Moghaddam, 2005.)